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THE VEGETATION ON BAUXITIC SOILS IN JAMAICA

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With nine plates

THE OCCURRENCE of a red-colored, mineral-bearing soil in the Greater Antilles has been recorded in the literature of the area for nearly one hundred fifty years. In the past the principal mineral element has been considered to be iron and its occurrence has been recorded in quantities of commercial significance. It has also long been recognized that these red soils of Jamaica, Cuba, Haiti and the Dominican Republic, generally called "terra rossa" are not particularly fertile for agricultural purposes. The agricultural worker has recognized that terra rossa soils also possess peculiar physical properties relative to erosion, water absorption, slickness to traction and texture. The farmer has acknowledged that special techniques are necessary for even marginal crop production and the botanists have learned of often unusual and endemic plants occurring on these soils.

For Jamaica, the first significant mention of aluminum ores in the red soil appeared in the memoirs of the first official Geological Survey when C. Barrington Brown described a "red ferruginous earth" widely covering a limestone formation as "principally a mixture of iron and alumina" (Sawkins Mem. Geol. Survey (Jam.) 167–8, 1869). While several analyses were made for mineral and agricultural purposes in the succeeding years, it was not until 1939 during the course of a systematic chemical investigation of soil types in Jamaica that the red soils of Jamaica were discovered to contain sufficiently high alumina and low silica percentages to make the soil a satisfactory source of commercial aluminum. Similar deposits are also known from Haiti (Goldich, S. S. & Berquist, H. R., Aluminous lateritic soil of the Republic of Haiti, W.I., U.S. Geol. Sur. Bull. **954–C**: 1948) and from the Dominican Republic (Goldich, S. S. & Berquist, H. R., Aluminous lateritic soil of the Sierra de Bahoruco Area, Dominican Republic, W.I., U.S. Geol. Sur. Bull. **953–C**: 1947). The analytical work of the Agricultural Chemistry division of the Department of Agriculture in Kingston, Jamaica, was directed to a study for improvement of the red, infertile soils of the limestone districts. The first efforts of analysis and improvement were applied at Grove Place in the parish of Manchester and

at Bull Savanna in the parish of St. Elizabeth. Similar soils in other parishes then came in for attention and it was in this way that Sir Alfred D'Costa, often incorrectly given credit for the discovery of alumina in Jamaica, secured the analysis of soils on his properties in the Lydford area near Claremont in St. Ann parish. An investigation directed towards commercial exploitation of these potential ore-producing areas was speeded by the war effort in the early 1940's. Post-war surveys later revealed ore in commercial quantities in other areas of Jamaica and between 1949 and the present time three industrial concerns have bought lands for the mining of aluminum-bearing ores. It is now recognized that a major portion of the land surface of the island of Jamaica contains aluminum-rich ore, a sizable percentage of this in commercial quantities, and that bauxite will constitute a major national resource of the island for many years to come. Bauxite and alumina together currently represent the second largest source of income for the island.

The commercial utility of the infertile "terra rossa" soils, however, does not remove the practical and scientific problems of the agricultural use of these soils, both now and in the future, and the botanical problems concerning the nature of the vegetation which occurs in such areas. In fact, commercial mining, using strip-mining techniques, poses other problems in the reclamation of the land and its proper use in the future. In this regard it is encouraging to note that the aluminum mining companies and the government of Jamaica, with its departments of mining, agriculture and forestry, are attempting a many-sided approach to the problems of adaptation and use of bauxite soils prior to and following mining, as well as independent of the mining processes. The legal position of mining operations in Jamaica is covered by The Bauxite and Alumina Industries (Encouragement) Law, Law 12 of 1950. The problems involved are clearly reflected in the Order made under the Law by the Governor in Executive Council on the 18th of September, 1950. This Order stated in part that "the recognized producer shall at all times maintain or cause to be maintained all lands . . . vested in or occupied by the recognized producer and which immediately before they became so vested or occupied were used for agricultural or pastoral purposes in as efficient a state of agricultural or pastoral productivity as such lands were immediately before they became so vested." The second condition of the order is that "so soon as may be after mining operations are concluded in any particular sector the recognized producer shall (a) restore every acre mined in such sector to the level of agricultural or pastoral productivity of such acre which existed immediately prior to the commencement of the mining thereof: or (b) if the Commissioner of Mines is satisfied that it is not economically practicable to comply with the provisions of sub-paragraph (a) of this paragraph as the Government of Jamaica may elect either (i) clear or reclaim one acre of land which immediately prior to such clearing or reclamation was not used for agricultural or pastoral purposes for each acre mined, in the relevant sector; or (ii) pay to the Government of Jamaica the sum of fifty pounds in respect of each acre so mined."

Thus legally the Government of Jamaica recognizes that arable land surfaces are limited in relation to an increasing population which basically has depended and will continue to depend upon its land for sustenance and profit. The law in the basic paragraph is an attempt to continue in useful condition lands temporarily withdrawn from the use of private citizens or small land-holders. The law recognizes that pastures or arable lands left idle in Jamaica, as elsewhere in the Caribbean, are soon reclaimed by noxious weeds, tenacious shrubs or forest growth, imposing on future owners tedious and expensive labor for land reclamation. The law specifies that once mining operations are concluded lands are to be restored to a level of production equal to that which existed prior to the mining process. A far-sighted law further recognizes that the mining of bauxite, being strip-mining in principle, may alter contours of the land in such a way that returning the area to its original condition relative to vegetation is impractical and the Commissioner of Mines, acting as the Government of Jamaica, may suggest either the reclamation of a comparable area of land in the vicinity or the payment of a fine. The goals of this legislation based on English law are to prevent the progressive development of large areas of waste land similar to the barren areas produced by strip-mining in many sections of the British Isles, as well as in the United States and other lands. The nature of the reclamation process has been left in the hands of the Commissioner of Mines who has worked with the cooperation and advice of specialists of the Departments of Agriculture and Forestry and with representatives of the mining companies. The representatives, individually and collectively, recognize the complexity of the problems involved. Thus there is in effect in Jamaica at the present time an honest effort, unique in the Caribbean and in the general history of strip-mining operations, to consider the problems and adapt the results for mutual benefit and for the present and ultimate well-being of Jamaica and its people.

The problems of revegetating mined-out bauxite areas are not simple. They involve acceptance of the fact that the soils are basically poor from the agricultural point of view and that in Jamaica, as in other heavily populated tropical areas, the lands have not received the attention and proper use deemed ideally desirable. The proper use of "terra rossa" soils has not been fully explored, but is currently receiving study and will necessitate continued study. The existing vegetation of bauxite soils is often unusual in habit, association and composition, as this study will show. Replacement of this vegetation by duplication may be difficult and may involve a series of carefully controlled steps. In fact, exact duplication of the existing vegetation may be undesirable and efforts are being made not only to revegetate the soil surface in mined-out bauxite areas, but to produce on these soils a vegetation of greater potential value than existed previously. In some cases this has meant the replacement of shrub-forest vegetation with pasture lands or the obverse replacement of pasture vegetation with forest trees following mining. Adjustments have to be considered relative to the contours developed during mining operations, for steep-sided pits negate the use of pasture grasses or require fencing, while

practices of fill or land movements depend on the economics of such operations as well as the machinery required. The relationship between the mineral content of the soil and the nature and growth of the vegetation upon that soil is admittedly complex, and clearly so in the relationship of these plants to aluminum ions. Thus, there are many problems on which representatives of mining, agronomy, forestry, chemistry and botany must share their knowledge. These are problems which are being worked out in Jamaica.

The authors of this paper, working under the auspices of the Institute of Jamaica, have undertaken a survey of the existing vegetation on bauxite soils in Jamaica. The senior author can call upon field experience in the bauxite areas of Hispaniola for comparison, but recognizes that further work is necessary on that island, as well. We have worked with the cooperation of the Commissioner of Mines and the directors and staff members in the Departments of Agriculture and Forestry. Permission to study at will the vegetation of the lands being mined or planned for mining in the future has been granted by the Reynolds Jamaica Mines and the Kaiser Bauxite Company. Over the past three years we have visited each area of mining operation during various seasons of the year. For comparative purposes, similar studies have been made of the vegetation on limestone outcrops adjacent to the bauxite accumulations. Studies are also under way on areas of bauxite accumulations to be considered for mining in the future.

Our efforts, as will be indicated subsequently in this paper, have been to determine the nature and the composition of the vegetation on known accumulations of aluminum-rich bauxite soils. We have studied and recorded the species of plants found in these areas, as well as the relative abundance of economic and academically significant species. Transects and population counts have been made for significant areas. Data are preserved as herbarium specimens collected at various seasons to insure material in flowering and fruiting conditions. Herbarium specimens, suitably indicated as to origin, are on deposit at the Institute of Jamaica and are available at any time for reference or study. Duplicate collections have been placed in the Herbaria of Harvard University, the British Museum of Natural History and the New York Botanical Garden. Additional specimens are available for other interested botanical organizations.

We wish to acknowledge our appreciation to the many individuals and organizations who have assisted materially in the progress of this study. Their cooperation and interest, their financial and intellectual support have made this study a pleasure to us and of benefit in the study of botany in the West Indies. We mention particularly the assistance we have had from Mr. C. P. deFreitas, Commissioner of Lands and Mines; Mr. B. E. Frayling, Deputy Commissioner of Mines; Mr. J. R. Elliott, Deputy Commissioner of Lands; Mr. J. F. Hart, Mines Officer; Mr. E. J. Gregory, Deputy Director of Agriculture; Dr. R. M. Arnold, Superintendent of Livestock Services; Mr. M. S. Motta, Senior Agricultural Officer; Mr. E. M. Brown,

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THE VEGETATION OF THE BAUXITE SOILS AND ADJACENT AREAS

Location of the Deposits

The survey conducted by the Geological Survey Department has been admirably summarized by Dr. V. A. Zans, senior geologist of the Geological Survey of Jamaica in a publication "Bauxite Resources of Jamaica and Their Development" (London 1954). Mr. Zans points out that through the efforts of the members of the Geological Survey and the geologists of the interested companies, commercial deposits of bauxite ore have been found in the parishes of Manchester, St. Elizabeth, St. Ann and Trelawny. Similar workable deposits are found in the parishes of St. Catherine, Clarendon, St. James and Portland. The other parishes either lack bauxite deposits completely or have only small accumulations of no commercial value. Currently, however, mining operations are limited to three areas in Jamaica. The Reynolds Jamaica Mines are operating on lands in St. Ann parish near Lydford Post Office. The Kaiser Bauxite Company operates areas of bauxitic soils in St. Elizabeth below Spur Tree Hill and south of the crossroads known as Gutters. These are the areas which have received our attention because of the diverse vegetation types represented and the different ecological conditions prevalent in the two areas. A third area of commercial operation is near Shooters Hill in the parish of Manchester, where the Alumina Jamaica Ltd. mines a more limited area similar in aspect to that operated by the Kaiser Company. We have given little attention to this area.

THE REYNOLDS AREA IN ST. ANN

The lands currently being mined by Reynolds Jamaica Mines are located chiefly among rocky wooded hills southeast of Lydford Post Office in the parish of St. Ann. The ore bodies occur primarily on a plateau in pocket-shaped hollows which range in elevation from 1100 to 1300 feet above sea level (PLATE I, FIG. 1). The surrounding limestone hills are heavily wooded with a rich array of hardwood tree species, an abundance of shrubs, numerous ferns and orchids occurring chiefly as epiphytes on trees on the limestone outcrops and a large number of weedy species of pantropical or Pan-Caribbean distribution occurring on lands once in agricultural or pastoral use.

This area north of Moneague has long been an area of extensive planta-

tions and estates, the names of which, in use today, go back over one hundred fifty years. Patrick Browne's map associated with his "Natural and Civil History of Jamaica" showns no named properties in the Moneague area in 1749 and Hans Sloane ("Voyage to . . . Jamaica" Vol. 1, 1707) mentions only the Moneague Savanna as a feature of the road or tract over Mt. Diablo to St. Ann's Bay. Edward Long in the History of Jamaica published in 1774 (Vol. 2, page 90) describing St. Ann parish avers that "the hills contain very few sugar works. The mould here is extremely superficial; and underneath lies a deep vein of a white marle, or hard chalk. The pimento loves this kind of soil; and vast woods of it over-spread the hills to a great distance from the coast. Behind this range of hills and mountains the land is diversified with open, level savannahs, environed by rocky eminences, or with little cock-pits. The soil of the latter is cultivated successfully with guiney-grass. The savannahs are covered with fern, and applied to no use. The road by Monte Diablo, in Sixteen mile-walk, leads into it on the south-east part, and is a mere avenue cut through the woods, there not being more than four or five settlements on the whole road. About five miles from Monte Diablo is the Rio Hoja, which, running about a mile and a half from its first spring, discharges itself into a large lake of immense depth." "The district of the parish intersected by these three avenues (Mt. Diablo, Pedro, Cave Valley roads) comprehends near one hundred and eighty thousand acres, as yet unsettled. In so vast a space, there must needs be a very great variety of soil, and numberless spots of very fine cultivated land. But, exclusive of a few fern savannahs, the whole of it is in its primitive forest, full of large cedar (*Cedrela*), mahogany and other valuable timber trees. The soil, over which the roads pass, is in general a reddish fat clay, intermixed with mould, or a black-shell mould."

Between Long's report of 1774 and 1811, when the first issue of "The New Jamaica Almanac and Register" to contain names of properties was published, the area attracted settlers and by 1810 such estates as Albion, Phoenix Park, Bellmont, Ramble, Grier Park and Crescent Park were evidently well established. Bel(l)mont and Crescent Park, two estate areas currently being mined for bauxite, were reported to have 51 and 99 slaves and 124 and 411 head of stock (including cattle), respectively. These lands have remained in large estates and in the hands of relatively few owners during the last century, and the land has been devoted to the raising of cattle with a few side exploits noted. The mention by Sloane and Long of savannahs and fern areas describes well the current situation with the limited fertile soils occurring as pastures and the shallower soils broken by small outcrops of limestone supporting the areas of fern (*Nephrolepis*). The wooded areas could not be regarded as of comparable productivity today, for while pimento is of scattered occurrence, cedar and mahogany have to a large extent been eliminated. Little information is available whether the depletion of these once richer forested areas came about through lumbering for purposes of construction, fuel for sugar mills closer to the coasts, or by generation after generation of slash cutting for fuel and

buildings by residents of the area. All three probably played a role and the shallow soils, underlain by marl, controlled replacement forest growth on the flat lands as the blocks of limestone in the "rocky eminences" limited forest replacement on the hilltops.

A few attempts at diversified crop agriculture have been attempted in the bauxite areas of St. Ann as indicated by the few pimento groves and casual plantings existing as remnant trees of cola, citrus, jak fruit, coffee and cocoa.

The area being mined by Reynolds in St. Ann parish today consists of numerous small glades or depressions partially filled with bauxite soils and low-elevation hills of loose limestone blocks of varying sizes. In recent years the flat lands have been devoted to pastures for cattle raising (Plate V, fig. 1). The limits of these areas are clearly defined in the vegetation, for the pastures stop at the rocky outcrop and the forests do not occur on the deeper soils. The margin of these two vegetation types is marked by shrub growth, in part natural and in part created by the convenience of the area for fuel wood cutting. Often these areas are covered with extremely dense stands of fern (*Nephrolepis biserrata*) creating a tangle difficult to penetrate. We have been unable to find an area of deeper soil supporting a forest. We wonder if such areas ever did exist or whether the deeper bauxite soils have always had a savannah vegetation.

The Environment

Vegetation can be interpreted in terms of soil types and climatic conditions as well as the plants which comprise it. Asprey and Robbins in their recent paper on the Vegetation of Jamaica (Ecological Monographs 23: 359–412. 1953) accept a method of vegetation classification which they state is largely one of convenience, recognizing both environment and species composition. Without discussing the vegetation of terra rossa soils specifically, they refer to them as "residual" soils "developed from weathering of hard white limestone through solutions and being typically coarse and porous in nature." They report that "although under conditions of poor drainage degraded forms of these bauxitic soils occur, they are usually much leached, acid, well oxidized and dehydrated. The red color is due to ferric oxide and their depth over the limestone plateaus varies greatly. There is no distinctive profile, but the surface has a high content of organic matter on which the agricultural value of the land depends." These observations, in our minds, do not appear to apply well to the pasturelands in St. Ann which are subtended by bauxite in commercial quantity. Profiles dug through these areas show very slight penetration of the root systems and relatively little organic content. The root systems of herbaceous plants and woody shrubs rarely penetrate more than eight inches and rarely do tree roots go deeper than two feet. The response of the vegetation to programs of soil improvement indicate natural low nutritional values for plant growth. The soil seems to be a

definite limiting factor in the development of better pasture areas or for the growth of forest trees. A soil analysis is available for the areas in St. Ann now being mined but none has been made for the mine area in St. Elizabeth. Samples of surface soil taken no deeper than six inches showed the following analysis which indicates the low level of essential elements:

pH	6.1
Organic matter	7.68 %
Phosphorous	0.019 — 0.036%
Nitrogen	0.48 — 0.53 %
Potassium	0.07 — 0.14 %
Calcium	0.14 %
Iron	0.84 — 1.63 %

The soil proved relatively rich in minor trace elements with no conspicuous deficiency noted.

The climatic factors are less restricting. Temperature records for the vicinity of Crescent Park and Lydford Post Office near the mines indicate a mild, even climate with a cloud cover on the hottest of days which aids in reducing transpiration and water loss. Rainfall in the Crescent Park area is favorable, being 66.2 inches per year with peaks in May and in October and November and distributed as follows:

January	3.9	July	2.7
February	3.6	August	5.1
March	4.1	September	4.9
April	4.2	October	8.8
May	9.9	November	10.2
June	3.3	December	5.5

Accepting the basic figure of four inches of rainfall per month as the minimum figure for optimum plant growth in the West Indies, the Crescent Park area had only four deficient months, distributed in pairs; January–February and June–July, and eight months over the minimum. These eight months are favorably distributed in growing periods of three and five consecutive months.

The Pastures

The pastures in the area of mining operations in St. Ann are relatively low grade. Without improvement, the average of these would currently support only one head of cattle for every five or six pasture acres. An examination of many of these prior to the mining operation revealed incipient invasion of woody shrubs and vines which could be kept under control only by constant effort (PLATE V, FIG. 1.) The forage plants were few in number and the unpalatable and therefore untouched grasses and herbs were numerous, if not dominant. The following list represents a fair sample of plants typical of pasture areas in the St. Ann area on bauxite soils prior to mining:

Andropogon glomeratus
Borreria laevis
Borreria verticillata
Cardiospermum grandiflorum
Cassia ligustrina
Cassia occidentalis
Cassia uniflora
Centrosema virginianum
Cissampelos pareira
Crotalaria incana
Desmodium axillare var. acutifolium
Desmodium canum
Dichromena ciliata
Drymaria cordata
Eleusine indica
Euphorbia heterophylla
Euphorbia hirta
Euphorbia hyssopifolia
Hydrocotyle asiatica
Mimosa pudica
Nephrolepis biserrata
Nephrolepis exaltata
Paspalum blodgettii
Paspalum conjugatum
Paspalum notatum
Paspalum paniculatum
Passiflora foetida var. hispida
Passiflora suberosa
Physalis pubescens
Phaseolus lathyroides
Polygala paniculata
Priva lappulacea
Pteris longifolia
Rubus jamaicensis
Setaria geniculata
Solanum nigrum
Stenotaphrum secundatum
Trimezia martinicensis

The following herbaceous invaders of over-grazed pastures in the St. Ann area which are to be distinguished from the noxious young shrubs capable of dominating pasture areas if untended. Of this list, *Ipomoea cathartica, I. tiliacea, Cissus sicyoides, C. microcarpa* and *Urechites lutea* are vines which become locally dominant through their habit of climbing over the forage grasses present. *Indigofera suffruticosa, Solanum mammosum, S. stellatum, S. torvum, S. verbascifolium, Rhytidophyllum tomentosum* and *Hyptis capitata* become stout plants dominant by size.

Ambrosia paniculata
Asclepias curassavica
Asclepias nivea
Bidens pilosa
Capsicum baccatum
Cissus microcarpa
Cissus sicyoides
Elephantopus mollis
Emilia sagittata
Emilia sonchifolia
Eryngium foetidum
Hyptis capitata
Indigofera suffruticosa
Ipomoea cathartica
Ipomoea tiliacea
Lobelia viridiflora
Mikania micrantha
Pavonia spinifex
Phyla nodiflora
Rhytidophyllum tomentosum
Salvia micrantha
Sida rhombifolia
Sida urens
Stachytarpheta jamaicensis
Thunbergia alata
Triumfetta hispida
Triumfetta lappula
Urechites lutea
Urena lobata
Verbesina alata
Wedelia gracilis

Untended pastures are invaded by seedlings of woody shrubs which develop extensively, shading or crowding out more desirable plants.

Casearia guianensis
Chrysophyllum cainito
Citharexylum spinosum
Cordia globosa
Eugenia axillaris
Eupatorium odoratum

Eupatorium villosum
Lantana camara
Lantana trifolia
Petitia domingensis
Psidium guajava
Psychotria nervosa
Psychotria pedunculata
Psychotria pubescens
Tournefortia hirsutissima

The stout woody vine *Tournefortia hirsutissima* reaches extreme lengths in pasture areas and its presence becomes a factor in limiting the pasture available to cattle and humans.

Programs of pasture improvement are under way on properties managed by the Reynolds Jamaica Mines. These programs include controlled grazing, the applications of natural and chemical fertilizers, weed control and reseeding. Such work is being conducted on areas planned for eventual mining, as well as on lands which lack sufficient ore bodies for commercial operation. The development and improvement of these pastures has achieved significant results in the few years of operation, allowing the grazing of cattle in larger numbers. Such a program certainly exceeds the spirit as well as the letter of the mining laws.

The Wooded Lands

The forest vegetation in St. Ann on lands operated by the Reynolds Jamaica Mines occurs on small limestone hills, outcrops of limestone rock and on the face of a small escarpment. (PLATE I, FIG. 1.) Asprey and Robbins' classification of "lowland type on limestone" would apply to the forests we have observed. As we have indicated, we have been unable to locate any forests on deep deposits of soil, although historical records indicate such forests might have occurred and subsequently been cleared of the trees. All the forests we have observed have been on limestone rock and have possessed only slight accumulations of soil. All have been cut over or severely culled and show the effects of human activity as well as that of nature's ravages of wind, especially hurricane damages, and time. The original forests in these areas must have been a rich mesophytic forest in which such trees as *Terminalia latifolia, Dipholis nigra, Ceiba pentandra, Cedrela odorata, Coccoloba swartzii* and *C. plumieri*, as well as other woody genera, occurred. *Swietenia* has not been seen as a natural component of these forests, although Long referred to the abundance of these plants in 1774. Likewise *Pimenta dioica* appears today to be residual plantation trees or occasional spontaneous plants from seed dispersal rather than a component of the mature forest. The forested areas studied are largely open, with relatively little herbaceous growth within the forest. Shrubs and herbs dominate the forest edges near the end of the limestone outcrop. Vines are infrequent except where fellings occurred and newer trees are developing. Epiphytes in abundance, including orchids, bromeliads and ferns reflect the ample rainfall. The dominant forest trees and those reaching the largest size are the following:

Adenanthera pavonina
Alchornea latifolia
Andira inermis
Casasia piricarpa
Cedrela odorata
Ceiba pentandra
Celtis swartzii
Coccoloba longifolia
Coccoloba plumieri
Coccoloba swartzii
Colubrina ferruginosa
Cupania glabra
Dendropanax arboreum
Dipholis nigra
Dipholis salicifolia
Esenbeckia pentaphylla
Ficus harrisii
Ficus ochroleuca
Ficus wilsoni
Guarea glabra
Hyperbaena laurifolia
Nectandra antillana
Nectandra patens
Ocotea staminea
Oreopanax capitatum
Peltophorum brasiliense
Petitia domingensis
Pimenta dioica
Pithecellobium arboreum
Pouteria multiflora
Simaruba glauca
Sloanea jamaicensis
Terminalia latifolia
Tetrazygia hispida
Tetrazygia pallens
Torrubia fragrans
Wallenia laurifolia
Xylopia muricata
Zanthoxylum elephantiasis
Zanthoxylum martinicense
Zizyphus chloroxylon

To the casual visitors to the forests of St. Ann the dominant plant of the lower stories in the forests may appear to be *Acidoton urens*, known locally as the "cowitch" or "scratch-bush." This plant possesses stinging hairs on most of the younger portions of the stems, on the leaves, flowers and fruits, and causes painful irritation when encountered. Equally abundant are the numerous species of *Psychotria* and *Salpixantha coccinea*. Other woody plants of small stature as well as diameters of less than commercial significance than the dominant trees are:

Allophylus cominia
Bauhinia divaricata
Calyptranthes chytraculia
Capparis cynophallophora
Casearia aculeata
Casearia guianensis
Casearia odorata
Colubrina ferruginosa
Daphnopsis americana
Drypetes lateriflora
Elaeodendron dioecum
Erithalis quadrangularis
Erythroxylum incrassatum
Eugenia disticha
Eugenia eperforata
Guettarda argentea
Hamelia ventricosa
Laetia thamnia
Maytenus jamaicensis
Palicourea domingensis
Phyllanthus coxianus
Phyllanthus inaequaliflorus
Picramnia antidesma
Rhamnus sphaerosperma
Rheedia sessiliflora
Viburnum villosum
Xylosma fawcettii

To determine the size and relative abundance of the forest trees in any given area of forest, we have made transect studies through forest areas selected for the purpose. Some areas were thought to be typical, others showed unusual elements in the flora. Our transects were made by marking off with cord an area 300 feet long and 60 feet wide, representing 18,000

square feet or approximately 41% of an acre. Because of the sharp inclines and the irregular footing in most of the areas studied, cross lines were run to allow counts to be accumulated from smaller areas and trees were marked to prevent chance recounting. The flora is well known to us, yet voucher specimens were collected in cases of doubt.

We recorded the occurrence of all woody species having a trunk diameter of four inches at breast height. Considering the density of the vegetation, even species of known economic potential have little chance of maturing if they are of lesser diameter. However, in several of the transects which follow, these species are indicated in separate listings. Diameters were recorded in categories of 4–6, 7–9, 10–12, 13–15, 15–20 and over 20 inches.

REYNOLDS AREA TRANSECT #1

North slope. Area from lower plain, level of drying kiln up sloping limestone face to level of plateau. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis nigra	11	1	8	2			
Simaruba glauca	8	5	1	2			
Brunfelsia americana	6	4	2				
Nectandra antillana	6	2	3	1			
Torrubia fragrans	6	2	1	1	1	1	
Casearia guianensis	5	5					
Celtis swartzii	5	5					
Bunchosia jamaicensis	5	3	1		1		
Daphnopsis americana	5	5					
Bauhinia divaricata	4	3	1				
Zizyphus chloroxylon	4	2	1			1	
Zanthoxylum martinicense	4	3		1			
Casearia sylvestris	3	1		1	1		
Sloanea jamaicensis	3	2			1		
Pithecellobium arboreum	3		1		1	1	
Ocotea staminea	3	2		1			
Cupania glabra	3	2	1				
Comocladia pinnatifolia	2	2					
Capparis cynophallophora	2	2					
Urera baccifera	2	1	1				
Coccoloba swartzii	2	1	1				
Dendropanax arboreum	1				1		
Oreopanax capitatum	1				1		
Andira inermis	1				1		

The largest of the trees encountered in this transect was 36 inches in diameter at breast height. This was an old and battered specimen of *Pithecellobium arboreum* which would not have produced a log of any value. Three trees with a marketable log over 12 feet long and 2 feet in

diameter were found, two of *Torrubia fragrans* and one of *Pithecellobium arboreum*.

The explanation for the greater number of useful trees and trees of larger size and greater frequency in this continuation of Transect #1 can be found in the nature of the rocky substratum onto which Transect #2 extended. This limestone hill consisted of large, irregular, loose blocks of stone. Climbing through the area of steep slopes necessitated the use of two hands. Lumbering in such an area, while not impossible, would be more difficult than cutting trees in the area of Transect #1 where the logs would be dragged to an opening and a roadway with much greater ease.

Reynolds Area Transect #2

A continuation of Transect #1 from the level of mining operation on the plateau to the top of the closest adjacent limestone hill. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	30	17	9	4			
Pouteria multiflora	19	9	5	4	1		
Torrubia fragrans	14	2	2	8			2
Daphnopsis americana	10	9	1				
Coccoloba swartzii	8	6	2				
Alchornea latifolia	6	5	1				
Cupania glabra	5	4		1			
Xylopia muricata	4	3	1				
Wallenia laurifolia	4	2	1			1	
Guarea glabra	5	4		1			
Bauhinia divaricata	3	3					
Pithecellobium arboreum	3			1			2
Capparis cynophallophora	3	3					
Guettarda argentea	2	2					
Allophylus cominia	2	1	1				
Comocladia pinnatifolia	1	1					
Zanthoxylum martinicense	1	1					
Oreopanax capitatum	1	1					
Hyperbaena laurifolia	1	1					

Another hill in the plateau mine area was selected for a transect study because of the several unique species found in the woods in considerable quantity. One of these trees, *Euphorbia punicea*, was the largest specimen either of us had seen, and apparently the largest on record. The plant has showy bright red bracts 1–1.5 inches long and possesses numerous flower clusters similar to the poinsettia. A specimen of *Euphorbia punicea* nine inches in diameter at breast height and thirty feet high was selected as the corner of a transect of one hundred fifty feet by sixty feet from the top of the hill where the *Euphorbia* grew to the margin of the forest at the lower edges of the hill. This transect showed the following tabular composition:

REYNOLDS AREA TRANSECT #3

Limestone hilltop above mine area on plateau. Hill forest dominated at the peak by specimens of *Euphorbia punicea*. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Pouteria multiflora	15	8	2	2		2	1
Nectandra antillana	9	1	8				
Omphalea triandra	6	4	1	1			
Alchornea latifolia	6	1	2	2	1		
Torrubia fragrans	5	1	2	2			
Casearia guianensis	4	2	1	1			
Oreopanax capitatum	4	1	2		1		
Comocladia pinnatifolia	4	4					
Exothea paniculata	3	3					
Andira inermis	3	2	1				
Rhamnus spherosperma	3	3					
Xylopia muricata	3	3					
Euphorbia punicea	2		2				
Coccoloba swartzii	2	2					
Pithecellobium arboreum	2			2			
Dipholis nigra	2	1		1			
Cupania glabra	2	1		1			
Zanthoxylum martinicense	1		1				
Capparis cynophallophora	1	1					
Terminalia latifolia	1				1		
Bauhinia divaricata	1	1					
Daphnopsis americana	1	1					
Zizyphus chloroxylon	1	1					

The "different" appearance of the forest vegetation on this hilltop was supported by the composition study of the transect above. This was accentuated when consideration was given to the shrubby growth and trees having a diameter of less than four inches.

The two hilltops represented in TRANSECTS #2 and #3 were small and the hills more or less conical in shape. Another hilltop in the same area had essentially the same degree of slope to the hilltop but the top was flat and of several acres in extent. This hill drew our closer attention because of the current and relic cultivation which had taken place on its slopes. The steep limestone slope had been cut and burned and crops of *Colocasia*, *Manihot*, *Musa* and *Cajanus* were under cultivation in some areas. Other areas once cultivated had grown up in a dense stand of *Solanum*, *Bocconia* and *Lantana* under trees of *Cecropia*. It appeared to be only a matter of time before cultivation practices would remove the woody vegetation on this hilltop.

The vegetation in this forest was largely undisturbed in the area of the transect. It was dominated, however, by the four very large trees with

spreading and dense crowns. One of these, *Oreopanax capitatum*, had a diameter of thirty-six inches at breast height and a trunk extending approximately sixty feet to the first branch. The large specimen of *Pithocellobium arboreum*, with a diameter of twenty-six inches, covered a ground radius of approximately seventy feet and the forest floor was covered with myriad seedlings. A specimen of *Dipholis salicifolia* was a matriarch of the hilltop with a large spreading crown and dense foliage. Seedlings of this aged tree dominated the undergrowth throughout the transect area.

Reynolds Area Transect #4

Flat top of limestone hill above stand of *Cecropia palmata*. Plot 150′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	14	5	3	5	1		
Dipholis salicifolia	11	5	3		1	1	1
Alchornea latifolia	11	4	3		2	1	1
Torrubia fragrans	9			7		2	
Oreopanax capitatum	8	1	1	4		1	1
Capparis cynophallophora	6	4	2				
Pouteria multiflora	6	3			2	1	
Wallenia laurifolia	6	3	2	1			
Dipholis nigra	6	1	4		1		
Coccoloba swartzii	4	4					
Comocladia pinnatifolia	4	4					
Pithecellobium arboreum	3			2			1
Zizyphus chloroxylon	3	3					
Terminalia latifolia	3		2			1	
Omphalea triandra	2		1		1		
Thrinax jamaicensis	1	1					
Cecropia peltata	1	1					

The density of young plants under the canopy of the forest trees recorded in the transect varied from the exposed margin to the interior. Variation was also seen relative to the exposure of the slope. A small quadrat twelve feet square was selected and studied in several of these transects and the number and height of the smaller woody plants recorded.

Quadrat #1 was located in the margin of the forest and the open grassy pasture of the woods reported in Transect #1. This transect contained seventy-one woody plants from one foot tall to over fifteen feet in height, but none of them exceeded two inches in diameter at breast height. Ten genera and species were found as recorded on the next page.

A second quadrat in a comparable area but with a southern exposure had a different composition with thirty-one species represented by sixty-eight individuals in an area twelve feet square. The plants encountered in this quadrat are recorded on the following page.

QUADRAT #1

Upper edge of TRANSECT #2. Western exposure. Plot 10′ × 12′.

	Total	1–3′	3–7′	7–15′	Over 15′
Acidoton urens	19	2		3	14
Piper jamaicense	10	1	1	8	
Malvaviscus arboreus	7			3	4
Capparis cynophyllophora	7	1	2	4	
Nectandra patens	7		4	3	
Guettarda argentea	6			4	2
Comocladia pinnatifolia	5	1			4
Coccoloba swartzii	5			5	
Rhytidophyllum tomentosum	3		2	1	
Bauhinia divaricata	2			2	
Total	71	5	9	33	24

In addition, a small portion of this quadrat contained a colony of *Polypodium polypodioides* growing on a rock and rotted log. The number of individual plants in this colony were too numerous to estimate.

QUADRAT #4

Nectandra antillana	20	*Capparis cynophyllophora*	1
Guzmania monostachya	13	*Pouteria multiflora*	1
Casearia guianensis	10	*Piscidia piscipula*	1
Cereus sp.	12	*Zizyphus chloroxylon*	1
Polypodium plumula	8	*Clusia* sp.	1
Eugenia sp.	6	*Dendropanax arboreum*	1
Hohenbergia sp.	4	*Ocotea floribunda*	1
Tillandsia valenzuelana	3	*Zanthoxylum martinicense*	1
Cupania glabra	3	*Ipomoea* sp.	1
Campyloneuron phyllitidis	3	*Cedrela odorata*	1
Comocladia pinnatifolia	2	*Rhipsalis cassytha*	1
Lonchocarpus sp.	2	*Anthurium grandifolium*	1
Chiococca parvifolia	2	*Campylocentron* sp.	1
Coccoloba swartzii	2	*Peperomia amplexicaulis*	1
Calyptranthes chytraculia	2	*Tillandsia tenuifolia*	1

The relationship between the sizable plants usually counted for a transect and the number of smaller plants of no economic, i.e., timber, value is frequently not taken into consideration. The development of any seedling into a mature plant is determined in nature, in Jamaican woodlands at least, by a number of factors including the presence or absence of competitors; the number of vines which may cause contortion or strangulation; the nature of the rock substratum on which the seedling obtains its start; the number of larger trees which may die or fall, limiting the growth of the younger plants, and the activity of termites in the area, to mention only a few.

One wooded area near the head of the conveyor belt at the Reynolds Jamaica Mines represented a mature forest area which, previous to mining operations, had been isolated by its location away from roads and bounded by rather difficult rocky slopes. During the course of our trips to this area this forest, now readily available to man on foot or in a car, has been attacked by machete and hoe. This forest proved to have a slightly different composition in its mature trees from the forests encountered and recorded in the transects just cited. The specimens were tabulated as follows:

REYNOLDS AREA TRANSECT #5

Northern exposure, summit of limestone hill. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Nectandra antillana	7	3	1	3			
Rhamnus sphaerosperma	7	4	2	1			
Ocotea floribunda	6	1	5				
Torrubia fragrans	6	1		3		1	1
Cupania glabra	4	2	1	1			
Guarea glabra	4		3		1		
Allophylus cominia	4	3	1				
Andira inermis	4	2		2			
Daphnopsis americana	4	3	1				
Zanthoxylum martinicense	3		1		1		1
Alchornea latifolia	3		2		1		
Casearia guianensis	2		1	1			
Oreopanax capitatum	2			1			1
Annona jamaicensis	1				1		
Phyllanthus coxianus	1	1					

With this tabulation complete, a line was then placed through the center of the transect and all plants within a distance of 1.5 feet on either side of the line were recorded. A total of 451 plants, representing 40 genera and 45 species, were counted. Because of the smaller size of the plants in this sample, only four of the 451 plants had appeared in the transect tabulation, although no conscious effort to avoid them was made in laying out the line.

The great diversity of the vegetation is, of course, one of the attractions which the vegetation of Jamaica and the Caribbean area in general have for the botanist. The diversity in genera and species is clearly indicated in the transects and quadrats compiled for the forested areas in the parish of St. Ann. The variations between hilltops, not only in aspect but in actual composition, are shown. Species and genera present, often dominant in one mixed forest on one hilltop, will be fewer in number or absent on the adjacent hill.

From an economic point of view, these are not profitable forests. The plants which make up the wooded areas are small in size and few in

number. Whether these areas ever contained what today would be considered marketable timber trees is a matter of conjecture. Even if Long's description of 1774 is accurate for the two species of commercial value which he mentions, *Cedrela* and *Swietenia*, some question must be raised as to whether these species could ever have dominated the area in view of the current mixed stands present. The trees which comprise the present forests are not important timber trees. Only a few, a dozen at most, of the species encountered in these areas are important trees and the majority of these are significant from the standpoint of cabinet woods alone. It is possible that in the past one hundred fifty years the marketable trees have been removed from the area either for lumber or for fuel. If that were so, one would expect a few gnarled old giants which, lacking good form or proximity to access roads, would have persisted. Such trees are rarely found and the "forest giants" are almost without exception trees of little commercial value and for that reason alone remain uncut.

QUADRAT #5

Top of hill near loading pit for conveyor belt. Plot 300′ × 3′.

Piper jamaicensis	51
Acidoton urens	45
Pilea crassifolia	38
Eugenia disticha	35
Rhytidophyllum tomentosum	27
Psychotria sp.	21
Eupatorium macrophyllum	21
Guettarda argentea	18
Eugenia axillaris	17
Nectandra antillana	15
Piper arboreum	14
Calyptranthes chytraculia	14
Bauhinia divaricata	12
Rhamnus sphaerosperma	9
Casearia guianensis	9
Coccoloba swartzii	9
Comocladia pinnatifolia	7
Eupatorium villosum	7
Torrubia fragrans	7
Viburnum villosum	7
Ocotea staminea	7
Miconia laevigata	7
Cupania glabra	6
Coccoloba longifolia	5
Daphnopsis americana	5
Blakea trinervia	5
Chiococca parvifolia	4
Hamelia patens	4
Andira inermis	4
Casearia odorata	4
Guarea glabra	3
Casearia sylvestris	3
Wallenia laurifolia	3
Paullinia jamaicensis	3
Salpixantha coccinea	3
Zanthoxylum martinicense	3
Xylosma fawcettii	3
Cestrum diurnum	3
Bunchosia swartziana	3
Allophylus cominia	3
Tetrazygia hispida	2
Xylopia muricata	2
Alchornea latifolia	2
Pithecellobium arboreum	1
Annona jamaicensis	1

The question might be raised as to why the trees which we studied in the forests of the St. Ann parish are no larger. Reasons for this lack of size were sought in a careful study of the areas represented by TRANSECTS #1 and #2. Possible answers were numerous. The area of the forest consisted primarily of limestone hills and the hills were composed of large

blocks of limestone more or less tumbled in position. Hill areas not of distinct blocks consisted of limestone deeply fissured, often in a checker-board pattern. This substratum which did not possess an accumulation of soil or humus represented an inferior spot for seed germination or for tree growth. Numerous seedlings encountered appeared to grow only to the extent of the stored food present in the cotyledons. Root development was poor and, with little humus to hold water, it appeared that most of the seedlings died from lack of available moisture, even though the area received an average of sixty-six inches per year. Forest litter, where such occurred, could be exceedingly dry during many of the seasons of our visits.

In the two transect areas studied, only four large trees could be considered as rooting in sufficient soil and that generally accumulated in the fissures of boulders. The vast majority of the trees were rooted on blocks of limestone with the roots extending around and below the blocks, as well as penetrating into the porous limestone. The effect of such a rooting habit was particularly evident in this area which received the effects of the last two major hurricanes in 1944 and 1951. Some of the largest trees were prostrate and rotting and an examination of the bases of these plants revealed that the blocks holding the trees had given way. The roots remained securely fastened to a tilted block of stone. It is apparent that the hurricane felled trees in this area of the Caribbean not by uprooting trees or fracturing trunks but by an indirect factor; i.e., alteration of the substratum.

Another factor in the relationship of tree species persistence to size and age is present in the limestone which, while hard, is eroded by the heavy rainfall in combination with the natural acids produced by decaying vegetative matter. The erosion of these blocks into a type of dog-tooth limestone is all too evident to the botanist who traverses these forests.

The effects of the vines and lianas, alone and in combination with the other effects mentioned here, in such a forest is also a factor in tree growth. Vines were not abundant in the very dense forests, but where openings occurred through natural or man-made causes, the vines appeared to scramble, with the aid of the smaller shrubs and saplings, into the tops of the larger trees. The extent and mass of some of these vines were surprising and a calculation of the weight involved in some of the larger woody vines would be a most imposing sum. Huge woody epiphytes or vines in this area included *Blakea trinervia*, *Clusia* sp., *Ficus* spp., *Solandra grandiflora*, *Rourea paucifoliata*, *Schlegelia parasitica* and *Ipomoea grisebachii*. Lighter weight vines or scrambling plants included *Chiococca parvifolia*, *Vernonia acuminata* and *Vernonia cinerea*, *Eupatorium odoratum*, *Clematis dioica* and *Notoptera hirsuta*. The effects of these plants would be felt through the dead weight involved, the concerted pull of the vines in any wind-induced movement of the forest canopy and in the tension exerted by the vine through its growth in various directions. It seemed obvious, from several trees we felled and others we observed in a contorted fashion, that the death or destruction of one tree entangled in

vines would be reflected on the others nearby and their growth pattern altered accordingly. In the younger plants the weight and pull of the young vines often contorted the sapling, removing completely the possibility of normal growth into a desirable timber tree. Strangulation of the host tree by the climbing vines was also apparent in the abnormal growth of the stems being squeezed.

A final effect was due to the activity of wood-eating termites in these forests. Termite tubes and termite nests were present on living and dead trees alike. Apparently any injury to a forest tree producing a break in the stem opened an avenue of attack from termites. Certainly the rapidity with which fallen timbers disappear is a tribute to the appetite and activity of the large termite population. These insects obviously play another role in the rapid destruction and alteration of potential timber trees in the tropics. The contrast is found in the temperate areas away from termite attacks where broken branches or trunk wounds would be healed over by callus tissue. Such self-repair is rarely encountered in the forests of the West Indies.

THE KAISER AREA IN ST. ELIZABETH

Location and Environment

The Kaiser Bauxite Company is currently mining bauxite soil in a dry, broad valley in the parish of St. Elizabeth (PLATE VI, FIG. 1 and PLATE VII, FIG. 1.) A view west from the company offices on Spur Tree Hill looking towards the Santa Cruz mountains and Malvern details the mining operation in the valley 1600 feet below. A road south from Gutters to Alligator Pond runs the length of this valley and the headquarters for the present mining operation is at a new location appropriately (but by coincidence) called New Buildings. In many aspects, from the techniques of mining to the vegetation involved, there are contrasts with the area in St. Ann operated by the Reynolds Mines. The same attention and techniques have been applied in our study to the pastures and forests associated with the bauxite deposits, but usually with less comfort. The entire mining area is lower in altitude, being only about 700 feet above sea level. Its location on the south coast of the island places it in the lesser southern rainfall division. The rainfall recorded during the year at New Buildings in contrast to Crescent Park totalled 44.75 inches, with lesser peaks in June and October–November.

The monthly rainfall has been recorded as follows:

January	2.42	July	0.72
February	1.82	August	4.80
March	0.94	September	4.23
April	3.37	October	6.35
May	3.75	November	10.31
June	5.19	December	0.85

The distribution of rainfall as recorded at New Buildings indicates that seven of the twelve months receive less than the four inches of rain considered necessary for optimum plant growth. Two additional months, August and September, receive only slightly in excess of the minimum. The number of consecutive months receiving above the minimum rainfall is also less in comparison with Crescent Park. These occur in August, September, October and November. The isolated month of June also receives above the minimum rainfall.

The temperatures in the valley also mount to greater heights and the evaporation rate is also high due to the extraordinary number of sunny days.

From the standpoint of climatic factors alone, the vegetation present in the Gutters valley exists under comparatively different conditions. As might be expected, the nature and composition of this vegetation is also different. Unfortunately, soil analyses are not currently available for these soils.

A map published in Patrick Browne's description of Jamaica of 1749 shows a "Pepper" plantation near Gutters and also a road south to Alligator Pond. Sloane apparently makes no mention of this area but Edward Long (The History of Jamaica 2: 185, 1774) reports that "about the foot of Mayday Hills the breadnut trees grow luxuriantly, and afford to the bordering settlements great abundance of nourishing fodder for their flocks." Long (l.c. 189) also refers to the area as "Labour-in-vain savannah" a term he states is "perfectly descriptive of its nature." He further comments that "In these parts there are but few sugar-plantations, though a great number of very fine penns for breeding horned cattle, horses, mules, sheep and goats, as well as poultry of all kinds."

Specific historical evidence for the properties now being mined is lacking. The New Jamaica Almanac citing statistics for the year 1810 apparently fails to list a single property in the immediate area of New Buildings. Plantations to the north toward Santa Cruz and the northwest foothills of the Santa Cruz Mountains supported 1529 and 1447 head of cattle, while plantations nearer by are cited as owning five and ten head of cattle. It seems obvious that high-quality pastures have never existed in the Gutters area.

Within the last few decades a special type of cultivation involving heavy mulching with quantities of guinea grass has developed and permitted the use of the land by small holders for the production of root crops, tobacco, pigeon peas and tomatoes. Large land holdings for the breeding and raising of cattle and other animals have largely disappeared. The lack of certain water supplies has reduced the emphasis on cattle raising with the result that few pasture areas comparable to those of the St. Ann area are to be seen. The lands now operated by the Kaiser Bauxite Company therefore involve fewer areas of pasture and more small crop fields now removed from cultivation.

The Pastures

A study of the areas to be mined which have been devoted to pastures revealed a very low grade forage present composed of a larger number of grasses than we encountered in St. Ann. A survey of these pastures revealed the following grasses:

Andropogon glomeratus	*Panicum adspersum*
Andropogon virginicus	*Paspalum caespitosum*
Axonopus compressus	*Paspalum fimbriatum*
Cenchrus echinatus	*Paspalum propinquum*
Cenchrus gracillimus	*Pennisetum purpureum*
Chloris petraea	*Setaria geniculata*
Digitaria sanguinalis	*Sporobolus indicus*
Eleusine indica	*Trichachne insularis*

Several of these species unpalatable to cattle had become dominant. While guinea grass, para grass and napier grass have been introduced in some areas and have remained as dominant stands when properly cared for, in adjacent areas they have given way to unpalatable species, reducing the value of the pasture. Weedy herbaceous invaders comprised essentially the same species as reported for pastures in St. Ann. Woody invaders of marginal pastures or pastures which have been neglected appear to grow faster and assume dominant roles much faster in this lowland area. One area under our observation for the years of this study changed so markedly that a quadrat study was made. This area was functional pasture in December, 1953. In January of 1956 (PLATE VI, FIG. 1) the shrubs had become so large and abundant that penetration was difficult and cattle tended to avoid the section. The area studied was located near a stand of logwood and the area selected for quadrat study was a hundred yards from the margin of this thicket. The following woody species were encountered in this effectively abandoned pasture:

QUADRAT #6

Kaiser property near New Buildings — area 101. Plot 40′ × 40′. The number of individuals of all woody species over 12″ tall are recorded in the table.

Haematoxylon campechianum	350	*Cordia globosa*	5
Lantana camara	44	*Urechites lutea*	4
Colubrina ferruginosa	42	*Ayenia pusilla*	3
Casearia guianensis	36	*Wissadula amplissima*	2
Eupatorium odoratum	26	*Hyptis pectinata*	2
Waltheria americana	23	*Crescentia cujete*	2
Melochia pyramidata	19	*Zanthoxylum martinicensis*	2
Triumfetta lappula	17	*Solanum verbascifolium*	2
Cordia jamaicensis	17	*Indigofera suffruticosa*	1
Croton lucidus	16	*Abutilon crispum*	1
Guazuma ulmifolia	9	*Psidium guajava*	1
Calliandra portoricensis	7		

The number and size of the plants which had invaded this pasture and developed to maturity in a period of two years is indicative of the problems of maintaining high quality pastures in Jamaica. While seedlings were present at the time of our first observation, cattle roamed and grazed in this area freely. Two years later the woody plants, especially the thorny *Haematoxylon*, constituted a real barrier. A total of 631 individuals over 12 inches tall in an area of 1600 square feet of pasture were counted. The largest plants encountered were a specimen of *Haematoxylon* 12 feet tall and 1.5 inches in diameter at the base; plants of *Lantana camara* (also spiny) and *Eupatorium odoratum* seven feet tall; specimens of *Hyptis pectinata* reached seven feet, as did spreading plants of *Solanum verbascifolium*. These latter two species spread prolifically once established in a pasture. The basic forage species of *Paspalum* and *Panicum* had given way to a dominance of *Andropogon* which cattle are reluctant to eat.

The sample represented by the QUADRAT #6 is not an exception to the general invasion and replacement affecting pastures in the valley of Gutters. Maintenance of pastures in this area requires constant care and prudent grazing practices.

The planting practices instituted by the Kaiser Bauxite Company on mined-out pits will be considered later. Within the first few years of operation, however, it appears as though limited pasture areas planted to good forage grasses carefully managed may persist as economical forage lands. (PLATE VII, FIG. 2.)

The Wooded Lands

The broad, flat valley around New Buildings contains low limestone outcrops rarely 100 feet high which support forests. (PLATE VI, FIG. 1 and PLATE VII, FIG. 2.) In general the limestone here is not in loose blocks, but exists as a solid, though checked, outcrop. Humus or soil is scarcely more abundant than in St. Ann, but is thick enough in places to allow tree growth upon the soil layer. The majority of these forests are secondary growth, having been cut continuously and now have few large trees other than specimens of *Bursera simaruba*. We were fortunate to find in one area of the Kaiser property a forest on a limestone outcrop which apparently has been well protected. No evidence of cutting was found on our first visit, although cutting has occurred subsequently. A transect study was made of this area and showed a composition as follows:

TRANSECT #6

Kaiser property, area 101. Forest on low limestone outcrop of 25 feet relief apparently protected and undisturbed. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis salicifolia	67	20	4	23	8	10	2
Ocotea staminea	8	6	1	1			
Hyperbaena domingensis	6	4		2			
Calyptranthes chytraculia	5	4		1			
Thrinax sp.	5	5					
Casasia longipes	4	2	1	1			
Guarea glabra	4	2	1	1			
Coccoloba proctori	4	1	1				2
Zanthoxylum insularis	4	1	2	1			
Coccoloba swartzii	3	3					
Wallenia laurifolia	2	2					
Omphalea triandra	2	2					
Lonchocarpus domingensis	1		1				
Comocladia pinnatifolia	1	1					
Bursera simaruba	1					1	
Sarcomphalus laurinus	1		1				
Piscidia piscipula	1		1				
Bauhinia divaricata	1	1					

The largest trees on this limestone forest represent some of the largest of their species known to us to exist in Jamaica. *Coccoloba proctori*, a new species, certainly fits that category but exceeds in two trees (36 and 24 inches in diameter at breast height) the largest specimens of this important timber genus known in the West Indies. The large number of *Dipholis* specimens, known locally as "bullet" would represent a significant forest resource if the pattern of distribution observed in this forest were repeated in the vicinity. Unfortunately this is not true and the occurrence of "bullet" here can only be taken as indication that the species does well in this area and should be considered as one of the species to be replanted on the mined-out pits.

The succession from pasture to forest land in the Gutters area is clearly marked in a number of woodlands. The shrubby growth described above which invades a misused pasture may assume control and is soon dominated by the logwood (*Haematoxylon*) in this dry area (PLATE VI, FIG. 1.) Apparently the only exceptions we have seen to this first step was a thicket of *Leucaena glauca*. In the majority of instances observed, however, the logwood was prevalent. In flat areas with a bauxite base, the logwood remained as the dominant tree and several of the old stands are being exploited today with logs collected for commercial use as a source of dye (PLATE IX, FIG. 1). On limestone, however, the logwood thicket soon becomes host to smaller plants of other tree species. In several logwood thickets we observed the development of specimens of *Nectandra coriacea*, *Wallenia laurifolia*, *Casasia longipes*, *Cupania glabra*, *Piscidia*

piscipula, *Metopium brownei*, *Coccoloba swartzii*, *Zanthoxylum insularis*, *Zanthoxylum flavum*, *Dipholis salicifolia*, and *Diospyros tetrasperma*. In time these simple or broader leafed species assume dominance over the compound leaves of *Haematoxylon* and apparently crowd out the latter. Dead and dying mature trees of logwood are common in limestone-based secondary forest thickets. These secondary forests are more diverse in their composition than the undisturbed forest previously described.

One limestone outcrop now supporting a secondary forest was distinguished as a former old field by the presence of stone walls traversing it. A transect in this area showed the following composition.

Transect #7

Secondary forest on limestone. Kaiser property, area #18. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20
Metopium brownei	31	24	6	1		
Bursera simaruba	12	6	5	1		
Haematoxylon campechianum	12	11		1		
Diospyros tetrasperma	10	10				
Lonchocarpus domingensis	7	7				
Dipholis salicifolia	6	6				
Simaruba glauca	5	4		1		
Tabebuia riparia	5	3		2		
Piscidia piscipula	5	5				
Zanthoxylum flavum	4	4				
Coccoloba swartzii	4	4				
Exothea paniculata	3	3				
Clusia sp.	3	2		1		
Gymnanthes lucida	2	2				
Allophylus cominia	2	2				
Picramnia antidesma	1	1				
Krugiodendron ferreum	1	1				
Bauhinia divaricata	1	1				

Consideration in the transect was limited to trees having a diameter of four inches or more at breast height. In addition to these established trees, representatives of the following genera and species were found in the same area.

Acidoton urens
Bunchosia swartziana
Casearia sylvestris
Celtis swartzii
Chiococca parvifolia
Clusia flava
Cordia globosa
Cordia jamaicensis
Croton linearis
Cupania glabra
Erythroxylon confusum
Eugenia sp.
Hamelia chrysantha
Phyllanthus nutans
Pisonia aculeata
Portlandia grandiflora
Psychotria myrstiphyllum
Schaefferia frutescens
Spathelia sorbifolia
Tabebuia angustata
Thrinax sp.
Xylosma sp.

One limestone outcrop was found supporting a secondary forest which extended into a pasture currently in use. A transect was made of this forest area beginning immediately behind the young shrub and tree area which could be distinguished as the pasture.

TRANSECT #8

Secondary woodland invading current pasture. Area 101 Kaiser property. Plot 300′ × 60′.

	Total	4–6	7–9	10–12	13–15	15–20	Over 20
Dipholis salicifolia	14	8	3	2			1
Diospyros tetrasperma	14	10	3	1			
Bauhinia divaricata	12	9	1	2			
Haematoxylon campechianum	9	8		1			
Coccoloba swartzii	9	7			2		
Ocotea staminea	7	6		1			
Gymnanthes lucida	6	5	1				
Bursera simaruba	4		1	2	1		
Amyris elemifera	3	2	1				
Wallenia laurifolia	3	3					
Simaruba glauca	3	1	1		1		
Calyptranthes chytraculia	2	2					
Piscidia piscipula	2	1	1				
Casasia longipes	2	1			1		
Picramnia antidesmia	2	1			1		
Esenbeckia pentaphylla	2		1			1	
Zanthoxylum flavum	2	2					
Oreopanax capitatum	2		1	1			
Metopium brownei	2			2			
Exothea paniculata	2	1	1				
Sarcomphalus laurinus	1	1					
Casearia guianensis	1	1					
Cupania glabra	1	1					
Capparis cynophallophora	1	1					
Coccoloba diversifolia	1	1					

The dry land forests of the Gutters area are more open in aspect than the forests of St. Ann. In spite of the relative abundance of light reaching the forest floor, herbaceous growth is scanty and consists primarily of a few species of ferns and *Peperomia*. No orchids have been seen in the areas examined. Epiphytes are numerous in local areas, but consist primarily of *Tillandsia recurvata* and *Tillandsia balbisiana*. *Syngonium auritum* occurs on the exposed limestone. The composition of these forests, primary or secondary, consists of a larger number of genera and species than were found in the forests of the wetter areas of St. Ann. The forests likewise appeared to have suffered greater ravages from man by being

cut for fuel and building purposes. The economic value of the limestone forests for lumber purposes is low.

A complete listing of the species found on lands to be mined, as invaders of mined-out pits and as occupants of the adjacent limestone outcrops to bauxite deposits is given in the second part of this paper for both the locations in St. Ann and St. Elizabeth.

THE RELATION OF THE VEGETATION TO ALUMINUM IN THE SOIL

The relationship of the plant to the soil has formed the basis for most agricultural research since man first cultivated plants. From such studies over a period of time has come our knowledge of root growth, structure and function, of mineral relationships to plant metabolism and growth involving major and minor elements, including trace elements and plant tolerances, preferences and responses to mineral elements, whether as deficiencies or in toxic abundance. As a companion study the botanist has often sought in the plant or the soil evidences of controlling factors in mineral-plant relationships. The recognition of plants as indicators of mineral components has attracted research and guided exploration for gold, iron and more recently for uranium. It is not unnatural, then, that we looked for plants as indicators of aluminum concentrations in our study of bauxite soils. The senior author, on previous field trips in Hispaniola, encountered several species of plants which are known only from depressions rich in bauxite and which are currently the site of mining operations. More recent collecting has not shown these plants on other than aluminum-rich soils. Whether such plants should be considered as indicators of aluminum soil or only plants tolerant of aluminum ions in the soil, in contrast to other species, remains to be established. Agricultural research dealing primarily with crop plants has shown that two considerations are possible for plants to be grown on soils rich in aluminum ions. These can be: A. plants susceptible to aluminum damage (i.e., non-tolerant species); or B. plants resistant to aluminum damage or tolerant of varying concentrations of aluminum in the soil.

It is known that certain plants will not tolerate any concentration of aluminum ions and are killed if grown on soils containing even small quantities of aluminum. Seedlings grown in soils or solutions containing aluminum ions show characteristic effects proved attributable to the concentration of aluminum. Slow growth and contortion of the shoot system comprise the obvious symptoms, but an examination of the plants shows root damage due to the "browning" of the roots or root hairs (Hoffert, G.N. & Carr, R.H. Accumulations of iron and aluminum compounds in some plants and its probable relation to root rot. Jour. Agr. Res. 23: 801. 1923). Continued deterioration of the root system results in starvation and eventual death of the plants. Previously much of this damage was attributed to the high acidity of the soil.

Information in this category is best known concerning the cultivated and

crop plants of the temperate regions rather than the natural vegetation of the tropics where aluminum ore is mined. Gilbert and Pember (Tolerance of certain weeds and grasses to toxic aluminum, Soil Sci. **39**: 425. 1935) reported that aluminum in the soil served to regulate competition between certain weeds and grasses. They concluded that grass seeds and seedlings were less affected by aluminum than dicotyledonous plants and so pasture areas under their observation developed pure stands of grasses, weed-free. (See also Shorland, F.B. The estimation of aluminum in pastures with special reference to soil contamination. Proc. Roy. Soc. N. Zeal. **64**: 35. 1934).

We observed the growth of pastures on areas of known bauxite concentration and the invasion and replanting of mined-out bauxite areas for these plant reactions. Although we are dealing with different genera and species, the results do not support the observations of Gilbert and Pember and of Shorland that aluminum itself in greater concentration limits the selection of species which invade or which could be planted.

It appears to be possible to establish three categories for plants which will grow on aluminum-rich soils. These are: 1. Plants requiring aluminum ions in their metabolism; 2. Plants known as "aluminum accumulators" which concentrate aluminum ions in plant tissues with visible but non-lethal effects; and 3. Plants which are tolerant of aluminum but collect little or only small percentages of aluminum in their tissues.

The role of aluminum as an essential element for plant growth has been investigated for a few areas and a few crop plants. Of particular interest is the fact that members of the Ericaceae, Moraceae and a great many ferns and Lycopodiaceae are considered now to require aluminum for proper development (Shorland, L.C. and Sommers, A.L. Studies concerning the essential nature of aluminum and silicon for plant growth. Univ. Calif. Pub. Agr. Sci. **5** (2): 57. 1926).

Vaccinium and *Rhododendron*, according to these reports, will not grow on control solution culture unless aluminum is added to the solution. Field work on the distribution of these two genera in Java supports the idea that aluminum is present where these plants occur and is absent where the species are absent (von Faber, F.C. Die Kraterpflanzen Javas in physiologisch-ökologisches Beziehung. Arb. Treub-Lab., Weltevreden 1. 1927). The distribution of *Vaccinium* species in the Antilles does not seem to follow the pattern described for the Far East. *Vaccinium* species do not occur on the deep bauxite soils in Jamaica but are montane plants, while *Rhododendron* is not native to the Antilles but species are cultivated at higher altitudes where temperature is more a factor than the absence of aluminum in the soil.

Several species of *Ficus* also require aluminum for normal development, according to the work of von Faber (l.c.). Many species of *Ficus* are present in Jamaica and the other islands of the Antilles, but occur apparently without special relationship to the concentration of aluminum ions. They are, however, a conspicuous feature of bauxitic pastures in Jamaica and clearly thrive in this environment.

The most detailed work on plants requiring aluminum has been done on ferns and club-mosses. Yoshii (Yoshii, Y. Aluminum requirements of solfatara plants. Bot. Mag. Tokyo **51**: 262. 1939) found that ferns in the Asiatic area grew most luxuriantly on soils rich in aluminum and that species of *Alsophila*, "*Aspidium*" and *Polypodium* failed to develop normally in the absence of aluminum.

The specific role of aluminum as an essential element is not completely understood. It appears to be associated with maturation, particularly of the fruiting portions of the plant and the setting of seed. Thus corn plants grown on aluminum-rich soils or solutions showed earlier flowering, earlier fruiting and heavier fruit production when compared with control plants (Sommers, l.c.). It is also suggested by literature of the field as reviewed by Hutchinson (Hutchinson, G.E. The Biogeochemistry of aluminum and of certain related elements. Quart. Rev. Biol. **18**: 1, 128, 242, 331. 1943) that aluminum may play a role in the uptake of water by plants. This factor alone may account for the heavier fruit production.

Aluminum may also have a catalytic effect on plant growth as shown in the case of citrus crops. *Citrus*, normally susceptible to damage by copper, is more highly resistant to copper injury when grown on soils rich in aluminum.

More attention has been paid to the ability of certain plants to accumulate aluminum ions as compounds, e.g., aluminum succinate within the tissues of the plants (Smith, H.G. Proc. Roy. Soc. N. S. W. **37**: 107–20. 1903). Such plants are called accumulators and are considered such when the concentration of aluminum ions equals or surpasses 0.01% of the dry weight of the plant. Accumulations as high as 8.5% have been reported in species of *Carpinus*.

The most comprehensive survey of the plant kingdom to determine the frequency of aluminum-accumulating plants in all groups has been completed and reported by Chenery in a series of papers (Chenery, E.W. Aluminum in the plant world. Kew Bull. **1948**: 173; **1949**: 433, 466). The original impetus for such a survey came when it was determined that the historic use of certain plants as mordants for dye work was due to the concentration of aluminum in the tissues. Further study of these mordant plants showed visible characteristics applicable to other aluminum-accumulating plants. In addition to the mordant properties, the presence of a characteristic yellowish green color in the leaves, the presence of pH sensitive anthocyanin pigments which respond to concentrations of aluminum by changing color (as in *Hydrangea*) and the presence of a characteristic bright blue-colored fruit, would indicate an accumulator species.

In his survey Chenery used a test reagent of ammonium aurine tricarboxylate in ammonium acetate, gum acacia and hydrochloric acid. Small fragments of leaf material when boiled in this solution caused a change in the orange reagent to scarlet, crimson or to opaque crimson, depending on the concentration of aluminum in the leaf tissue. It has been shown by other workers that the concentrations of aluminum within the plant are

greatest in the roots, becoming less in the stem and leaves. A few plants accumulated aluminum in the roots and failed to transport the ions beyond the root system. L. J. Webb (Aluminum Accumulation in the Australian-New Guinea Flora, Austral. Jour. Bot. 2 (2): 176–196. 1954) has recently reported that "variation in results occurred when samples of the same species were tested from different localities, or when different parts of the tree were tested." In various species Webb reported positive accumulator reactions from one locality when negative from another, or a positive reaction from the bark but negative from the leaf. In *Quintinia sieberi* plants which establish themselves as epiphytes, reactions were negative in young plants, but older ones exhibited a positive test. A second species lacking the epiphytic habit was positive in reaction. Webb concluded that "these variations suggest that aluminum accumulation is not always obligatory among individuals of some species."

The results of Chenery's extensive survey and Webb's comprehensive coverage of a local flora must be considered as being on the conservative side as much of the work was done with dried and herbarium materials, involving only fragments of single plants.

In neither Chenery's nor Webb's work is any evidence given of the presence of aluminum in the soil where these plants were growing. We regret that we have not had the opportunity of applying Chenery's techniques to a survey of the plants growing on bauxite areas of known concentration in Jamaica. Such tests would demonstrate either accumulator or tolerant species.

Webb has listed the families which are known to contain species which accumulate aluminum based on the reports of his own research and that of Hutchinson and Chenery. These are Monimiaceae, Lauraceae, Violaceae, Polygalaceae, Vochysiaceae, Crypteroniaceae, Geissolomaceae, Proteaceae, Theaceae, Myrtaceae, Melastomaceae, Rhizophoraceae, Scytopetalaceae, Euphorbiaceae, Cunoniaceae, Escalloniaceae, Hydrangeaceae, Celastraceae, Icacinaceae, Octoknemataceae, Juglandaceae, Diapensiaceae, Symplocaceae, Diclidantheraceae, Loganiaceae, Apocynaceae, Rubiaceae, Gentianaceae and Lentibulariaceae. Webb considers the data compiled and discusses it along biochemical ecological and taxonomic lines. He suggests as cited in his summary that "A high aluminum content of the organs of accumulating plants appears to be associated with normal metabolism." Further, that "obligate accumulators are confined to leached acid soils from a variety of parent materials, in comparatively high-rainfall areas."

Few of the families which contain accumulator species occur in Jamaica and fewer still on bauxite soils. Chenery points out that the greatest *number* of accumulator species have been found in the Rubiaceae and the Melastomaceae, both families represented in Jamaica, and that the greatest *percentage* of accumulator species belong to the Diapensiaceae and the Symplocaceae. In the latter two families all species tested proved to be accumulators, and for the Symplocaceae Webb found eight species as accumulators of the eight species tested. *Symplocos* occurs in the West Indies and three species have been reported from Jamaica but are not

associated with bauxite soils. Such genera containing known accumulating species as *Morinda, Oldenlandia, Lasianthus, Psychotria, Miconia, Ternstroemia, Cyathea, Dicranopteris* (*Gleichenia*) and *Lycopodium*, do occur in Jamaica. A few of these genera have been found on bauxite soils but in no case are they limited to bauxite soils. They are, in fact, much more abundant elsewhere, indicating that aluminum in bauxitic concentrations is not necessary for their growth, and that other factors control their distribution in Jamaica. No species of these accumulator genera are restricted to bauxite soils. Certainly the observations of Chenery and Webb that acid soils and high rainfall are required for high accumulator species cannot with ease be applied to the composition and distribution of the vegetation found on bauxite soils in Jamaica.

Webb uses the data regarding accumulator species for practical taxonomic considerations. He reports that the "recorded accumulators are mainly restricted to what are usually regarded as the more primitive groups in dicotyledons and filicales, suggesting that accumulation is a physiological relic in these groups." He points out that "with the exception of the Rubiales, all the well-developed accumulating orders are confined to the Archichlamydeae or the primitive sections of Metachlamydeae. Accumulation is erratically developed in *Rubiales* and only slightly in other Metachlamydeae." If it can be assumed that aluminum accumulation is associated with normal metabolism and therefore characteristic of those species, then until further tests are made, the vegetation which occurs on bauxite soils in Jamaica must be considered as species which are neither accumulators nor non-tolerant of aluminum concentrations. Instead, it appears that the bauxite flora of Jamaica consists of plants which are unaffected by aluminum and tolerant of its presence.

Webb also suggests that accumulation of aluminum seems to be a useful character to supplement other data in the clarification of some taxonomic problems. He cites examples of *Helicia* and *Finschia* where the proper affinities of the species are suggested by the accumulation of aluminum. Manske and Marion (Manske, R.H.F. & Marion, L. The alkaloids of Lycopodium species. Canad. Jour. Res. B. 20: 87, 153. 1942; 21: 92. 1943; 22: 1. 1944) found that in *Lycopodium*, where the color of the plant is often used as a supplementary character for dividing the genus, the color was a direct indication of the percentage of aluminum in the tissues.

We have looked in vain for an application of Chenery's suggestion of blue fruit, yellow-green color to the foliage and pH-sensitive anthocyanin pigments in the vegetation on the bauxite soils. Such plants occur in Jamaica, but without correlation to bauxite. As we have indicated, in the course of our work to the present we have been unable to find undisturbed forests or savannah vegetation on the deposits of bauxite of known concentrations. Explorations by the bauxite companies continue in more remote parts of the island, such as the John Crow Mountains and the Cockpit country where future expansion of the mining operation will take place. In such areas we still hope to encounter a vegetation which

will demonstrate the existence of endemic species related to bauxite soils or counter effectively the slight evidence on hand from the deposits in the Dominican Republic and Haiti. To the present we have found no species characteristic of bauxite soils, nor have we demonstrated that the vegetation of adjacent areas currently not found on the bauxite deposits will not grow on the bauxite soils. To the contrary, the invasion of plants from adjacent areas on barren, mined-out pits and the plantations established in these pits indicate that factors other than the concentration of aluminum will control the success or failure of these species on bauxite.

MINING TECHNIQUES IN JAMAICA REGARDING BAUXITE ORE

Strip-mining techniques for the extraction of bauxite ore in Jamaica are relatively simple in contrast to those used in areas of greater amounts of overburden. The deposits in Jamaica encountered to the present are all superficial, the bauxite having been deposited in pits on a hard limestone base. The nature of these deposits is well described and illustrated by Zans (l.c. 318, plates III, IV and VI), who reports that bauxite deposits are "confined either to circular or oval declines (cockpits) and large elongated 'glades' (bowl or catchment deposits), or to larger, uneven depressions in limestone plateaux blanketed by undulating sheets or lenses of bauxite. Smaller deposits occur in pockets, pipes, and irregular solution cavities on the hillsides of the honeycombed limestone and also filling the fissures and brecciation zones." "All the deposits are surface accumulations, covered only by a thin layer of soil and sparse vegetation." "The deepest pocket drilled in Jamaica is 114 feet deep in a deposit near Williamsfield in the parish of Manchester. Deposits less than five feet in thickness are not considered workable, and the average minable thickness is of the order of ten to thirty feet. The tonnage of the individual commercial orebodies varies from a few thousand to several million tons."

In opening the deposits for mining the top soil ("overburden") is removed by bulldozer or dragline scraper and set aside for replacement once mining operations are completed (PLATE VI, FIG. 2.) The removal of the overburden is in part a practical operation and in part a consideration for the future reclamation of the mined-out pit. The overburden contains remnants of the plant life, the root systems and the accumulation of organic material, but consists of the same chemical, i.e., aluminum composition as the lower deposits. Processing of the overburden would require ashing of the organic material. Removing and stockpiling the overburden avoids the necessity for this complicated operation.

With the overburden set aside for future use, the ore is removed by mechanical excavators, power shovels, drag lines or scrapers (PLATE I, FIG. 2 and PLATE VI, FIG. 2.) The ore is then hauled to transportation centers by bottom- and rear-dump trucks. Equipment used and methods of transportation vary with the companies; however, both Kaiser and Reynolds dry the ore, removing eighty to eighty-six percent of the moisture

contained. The dried ore is then exported for further processing to alumina and metallic aluminum.

The nature of the depression that remains following removal of the bauxite ore varies with the size of the ore body and with the contour of the hard limestone base. Minable deposits average ten to thirty feet in depth, but a few located in small limestone "cockpits" were deeper, the resulting depressions being steep-sided. The larger the ore body, the less precipitous were the borders of the depression and the easier could be the early steps of pit reclamation. In general, the practice of the companies appears to be to alter steep-sided depressions where possible by blasting or by using tractors to ease material into the hole. Contours of the larger depressions are smoothed with tractors and bulldozers. (Plate V, fig. 2 and Plate VII, fig. 1.) Overhangs are removed and dangerous slopes fenced off. Once the contour has been adjusted, the overburden is replaced and leveled. Distribution of the overburden is made as uniform as possible and the overburden is contoured with the greatest possible agricultural utilization in mind. The soil surface is then processed, generally using sheepsfoot rollers but occasionally by discing, harrowing or ploughing. Contours are established and attempts at erosion checks are made. (Plate II, fig. 2 and Plate VII, fig. 1.) The problems of re-establishing vegetation on these naked mined-out pits are evident. Soil samples from the bottom of several pits have been analyzed and show an organic content of 0.10% to 0.15% and a nitrogen count from 0.00% to 0.033%. The pH of these soils varied from 5.9 to 6.1. Potassium counts averaged 0.7% and phosphorous 0.41%. Even with the replacement of the overburden, the organic content remained very low. Without the proper surface preparation the soil is very compact.

SUCCESSION ON THE EXPOSED MINED-OUT PITS

We have been fortunate in having the cooperation of the managers and the agricultural specialists of both the Reynolds Jamaica Mines and the Kaiser Bauxite Company in the course of our investigations. At our suggestion and with the approval of the Commissioner of Mines, control areas have been established in the mine areas. Mined-out pits have been allowed to stand fallow to permit our observations concerning the natural invasion and succession in mined-out bauxite pits. (Plate II, fig. 1).

A complete list of the plants which have appeared as invaders of the mined-out pits appears as a tabulation in the second part of this paper. Within six months from the cessation of mining operations in the control pit at the Reynolds Mines sixty-one species of plants were recorded as established within the pit. A definite zonation was evident with vines, primarily *Cissus sicyoides*, *Mikania micrantha*, *Ipomoea cathartica* and *I. tiliacea* on the slopes and the abundance of herbaceous and woody species in the silted-in center depression. The greater number of invaders appeared on the area where the overburden had been replaced, indicating both the comparatively greater fertility of this soil and the possible presence of weed

seeds in the overburden. Additional species which have not been seen in the control pit were found in other pits which received special plantings. It was of interest to note that several species of plants not recorded elsewhere in the area appeared in the mined-out pits. These were *Aster exilis*, *Lactuca jamaicensis*, *Crepis japonica*, all herbs, and *Ochroma pyramidale*. Woody plants which were among the early invaders were *Ficus suffocans*, *Bocconia frutescens*, *Zanthoxylum martinicense*, *Cordia globosa*, *Petitia domingensis* and several species of *Solanum*. *Zanthoxylum martinicense* and *Petitia domingensis* were given special significance as the woods of both species are used for light construction work on the island. During the first year of observation, changes were recorded in the relative composition and the size of the plants. Many species disappeared after one seed generation, but plants known elsewhere as persistent pan-Caribbean weeds remained and often increased in number. Species of *Sida*, *Solanum*, *Stachytarpheta*, *Eupatorium*, *Lantana*, *Borreria* and *Cassia* flourished. *Ambrosia* became locally abundant. The vines, especially *Cissus sicyoides* and *Ipomoea cathartica*, fruited heavily and spread rapidly for most of three years, forming a tangle over the ground which impeded travel but seemed to have little effect on the erosion rate of the area. Natural decline of these two species has already set in as other plants have appeared on the slopes of the control pit.

The growth of *Petitia domingensis*, a useful timber tree, has been very slow. *Zanthoxylum martinicense*, however, grew rapidly and has continued that rate. (PLATE III, FIG. 1.) Additional specimens of this species have been recorded since the original observations, and several of these plants increased in height by nine feet between two of our visits, nine months apart. *Ochroma pyramidale,* which was not present in our original observations, appeared subsequently and now towers over the vegetation in the control pit (PLATE III, FIG. 2). Specimens of *Terminalia latifolia* also appeared in the course of our observations and have grown prolifically since. Ferns, particularly *Pteris longifolia*, have appeared in quantity but grasses are scarce, the most abundant plants being *Stenotaphrum secundatum* and *Andropogon glomeratus*. *Stenotaphrum*, like *Cissus* and *Ipomoea*, appears to dominate areas by the long, sprawling habit developed, but these plants have not rooted naturally along the runners and hence are of slight value in retaining the soil.

No attempts at following succession were made on pits which had been planted, since cultivation practices in these areas altered the invading vegetation. One of the goals of the succession study on a controlled pit was to locate if possible a naturally established, ground-covering plant which would reduce erosion. Three plants which were prominent in pits other than our control pit appear to serve this purpose. They are *Mimosa pudica*, a legume capable of enriching the soil, *Borreria laevis* and *Wedelia fragilis*. Both *Mimosa pudica* and *Borreria laevis* seem well suited for the purpose, being low, prostrate plants which seed abundantly and cover well. The latter is eaten by cattle and could be considered low forage.

However, it has been suspected of producing toxic effects and should be encouraged only with this caution in mind.

As might be suspected in the drier area of the Kaiser operations in St. Elizabeth, the rate of invasion was slower than at Reynolds and the number of species at a given time was fewer. Thus, in six months following the cessation of mining operations, a control area on the Kaiser property had only forty-one species of plants. These were fewer in individual representatives and much more scattered in distribution. Subsequent changes at Kaiser have not shown the same loss of species and in our last visit all the species encountered in previous visits were still to be found. Additional invaders have been few. Grasses such as *Setaria*, *Andropogon*, *Digitaria*, *Cenchrus* and *Stenotaphrum* are more numerous and specimens of *Haematoxylon* and *Lantana* appear to be the most conspicuous elements. *Haematoxylon* is probably the most abundant plant in the valley near the mining operations and with its samara-like fruits is obviously distributed widely. The logwood, therefore, must be considered in any attempts to maintain pastures or woody plantings in the mined-out pits. No plants of potential economic value have appeared spontaneously in the Kaiser pits.

The relative fertility of the overburden when stockpiled adjacent to the mining operations has drawn the attention of visitors to the mine area. It must be pointed out that the overburden contains not only the organic matter and the roots, but the fruits and seeds of the area. Thus the rapid covering of relatively luxuriant vegetation on the stockpile of overburden is mostly indicative of the presence of plant life and propagating material in the soil. At the Reynolds Mine area we have been able to watch the development on stockpiles of overburden of twenty-three species of plants which in four years of observation have not appeared spontaneously in the mined-out pits. These plants include five pasture grasses as well as the following potentially valuable economic plants: *Musa sapientum*, *Cecropia palmata*, *Ricinus communis*, *Hibiscus elatus*, *Ceiba pentandra* and *Pimenta dioica*. In the Kaiser area none of the plants recorded from stockpiles of overburden is different from those appearing as natural invaders of the mined-out pits. Of the natural invaders, only *Haematoxylon campechianum*, the logwood could be considered of any economic value.

REPLANTING THE MINED-OUT PITS

The majority of mined-out pits on the Kaiser properties have been of such contours to allow development as pasture areas. In these plantings a variety of pasture grasses have been attempted by seed and rhizome propagation. Most have been established as pure stands. Guinea grass (*Panicum maximum*) has proved the most successful and controlled grazing has already been permitted on several of these reclaimed pits. (PLATE VII, FIG. 2.) Pangola grass (*Digitaria decumbens*) is now being tried both for forage and erosion control and looks promising. Para grass (*Panicum purpurascens*) and Wynne grass (*Melinis minutiflora*) have not, to our view, been so successful. In all pasture areas there has been

an invasion of weed herbs and woody species and these have necessitated manual labor to maintain the pastures.

The Kaiser Company has also devoted some of its reclaimed pits, generally those of steeper contours less suitable for cattle, to reforestation. In general these have received mixed plantings, although some nearly pure stands have been set out. The seedlings are obtained from the Forestry Department, usually from their nurseries at Spanish Town on the south coast, to supply plants which have been started and grown under comparable conditions of temperature, exposure and rainfall. Forest tree plantings have been primarily of *Swietenia mahogani* (mahogany), *Cassia siamea*, *Hibiscus elatus* (mahoe), *Cedrela odorata* (cedar), *Tectona grandis* (teak) and a very few specimens of *Melia composita*. *Swietenia*, well adapted to the environmental conditions of the area, has done well. Plantings two years old average six feet in height and about an inch in diameter at breast height. Some infestation of tip borers has been experienced. The habit of these plants is normal and little pruning appears necessary. The few specimens of *Melia composita* have shown the most rapid growth rates, with specimens two years old reaching now to over twenty-seven feet. In all cases, these have been planted in the lower portions of the depressions. *Cassia siamea* is little grown as a timber tree in the New World, but is often planted as a source of building poles, fuel and lumber in Asia. When interplanted with *Hibiscus elatus* or *Swietenia* these trees have done well and since they will mature more rapidly, will be cut as a source of fuel and as a means of thinning the plantings. (PLATE IX, FIG. 2.) Some trees of *Cassia siamea*, three years after planting, are now twenty-five feet tall with diameters of eight inches and are in flower.

A few plantings of economic or agricultural crop plants have been attempted without outstanding success. Lime and other citrus plants have not adapted themselves to the area and survivors have tended to branch from the base to produce dense and crowded crowns. The pigeon pea, *Cajanus cajan*, has been grown on the mined-out pits but has not fruited so heavily as control plants on undisturbed soils.

More recent plantings have been on deeper soils in mined-out pits and greater attention has been given to soil preparation. One mined-out pit has been devoted to test plantings of peanuts, cassava, sweet potatoes and a variety of garden vegetables. Commercial fertilizer has been used and the crops appear to flourish vegetatively, although a complete crop cycle has not elapsed. On well-tilled soil the peanuts have flowered and produced small fruits which at the time of our last visit had not matured. A variety of fruit trees including breadfruit and mangoes have also been planted in this area.

The development of plantings of *Hibiscus elatus* from the foresters' viewpoint has been most disappointing in the St. Elizabeth area. Originally our observations indicated a high percentage of loss following transplanting and of the survivors a majority suffered die-back. (PLATE VIII, FIG. 1.) Such a response has been attributed to the toxic effects of aluminum ions in the soil. Our initial reaction was that this significant timber species in

Jamaica was not adaptable to reforestation of mined-out pits. However, in subsequent visits it has been apparent that not all the plants suffering from die-back necessarily died. In fact, a majority of these sprouted from the base and presented a problem of a different nature. Additional observations have shown that if mahoe seedlings are given proper care between digging and replanting, losses can be reduced. Furthermore, while watering of transplanted trees is impractical, planting times can be adjusted to rainy periods and survival percentages thus further increased. Mulching would also be helpful. The problem of managing large plantations of trees which have suffered die-back and have branched from the base is, however, an imposing one. Obviously several trunks cannot be permitted. (PLATE VIII, FIG. 2.) Laborers must be trained in proper pruning practices regarding these plants. In general the mahoe growing in mined-out pits in St. Elizabeth, in contrast to those planted in St. Ann, have not grown in height at the expected rate. Instead the average plant has developed a much more dense crown and has branched freely from the lower region of the trunk. Crown development in width and density has dominated trunk development. Again the question is raised of the economic feasibility of pruning branches for trunk development.

Hibiscus elatus as a timber tree has not proved as satisfactory on the mined-out bauxite pits in St. Elizabeth as it has on comparable pits in St. Ann and on other terrain elsewhere in Jamaica. From information so far obtained, the climate of the valley near Gutters is not ideally suited for the growth of the mahoe as a timber tree.

Maintenance problems of young forest plantations in St. Elizabeth seem slight in comparison with those encountered in St. Ann. Most evident is the lack of vines which strangle or contort the saplings and the cleaning of forest plantations in St. Elizabeth can be regarded as a minor expenditure.

In the operational area of Reynolds Jamaica Mines in St. Ann (as in St. Elizabeth) both pasture development and forest planting has been carried out. Only a few of the mined-out pits have been considered of suitable shape for the development of new pastures. In these either guinea grass (*Panicum maximum*) or para grass (*Panicum purpurascens*) have been planted primarily by rhizome propagation. One area is documented in photographs which show the contours of the valley prior to and during mining operations and after reclamation. (PLATE V, FIGS. 1 and 2.) A survey was made of this area before mining operations began to record the quality of the pasture in terms of the plants present. Comparatively, the area which would carry at most one cow for every five acres before mining operations began, will be expected to supply forage for at least one cow for each acre now that the pasture is well established. Reclamation in this area has increased the available pasture, improved its quality and definitely improved the contour of the area by an increase in the level acreage.

More recently, para and guinea grass clumps have been planted in steeper contoured pits along with forest trees. It has been demonstrated that the clumps of grass serve effectively as checks to the erosion which was destroying many of the forest tree plantings. (PLATE II, FIG. 2 and

PLATE IV, FIG. 1.) Pangola grass (*Digitaria decumbens*) is also being tried in the vicinity to rebuild overgrazed pastures and as an erosion control.

In the mined-out pits of steeper contours, where pasture establishment is not possible, forest trees have been planted. The nature of the environment in these areas has been deemed most suitable for mahoe (*Hibiscus elatus*) and fruit trees. *Cassia siamea* and *Swietenia mahogani* have not been tried in the area. It is hoped that future planting plans will include prickly yellow (*Zanthoxylum* spp.), fiddlewood (*Petitia domingensis*), broadleaf (*Terminalia latifolia*) and balsa (*Ochroma pyramidale*), which have proved in the control pits to be adaptable to the area. As these timber trees are valued in local industry, plantations of these will find a ready market when mature.

By contrast with the plantings in St. Elizabeth, the mahoe in the Reynolds Area of St. Ann adopts an upright although slender habit and has, in all cases observed, produced a fine trunk branching at normal, i.e., higher levels. Larger plants now two years old are twenty feet high with trunk diameters of five inches and are in flower. (PLATE IV, FIG. 2). Die-back was originally evident in the early plantings of mahoe and the avocado in the St. Ann area, but such die-back seems more readily controlled by giving greater care to transplanting practices and to the time of planting in relation to the rainy months.

Plantings of avocadoes (*Persea americana*) called "pear" in Jamaica have proved successful on the reclaimed pits. (PLATE II, FIG. 2 and PLATE IV, FIG. 1.) With the selection of the best strains or by budding the trees once the root system is established, an important economic crop can be assured.

In the moist climate of the Reynolds operations, *Pinus caribaea* shows signs of promise as a timber tree. Small experimental plantings two years old show excellent growth to five feet.

The workers of the mines have added materially to the experimental selection of plants for the mined-out bauxite pits through surreptitious planting of a variety of vegetable crops. We have followed the illegitimate gardens with interest and have observed that corn (*Zea mays*), cabbage and beans have done well. Less successful have been plantings of yams (*Dioscorea*), taro or "coco" (*Colocasia*) and cassava (*Manihot*). Pumpkin vines produced an abundant crop.

The problem of erosion control has been a major one in this area of sixty-six-inch rainfall. A test planting was made of kudzu (*Pueraria lobata*), but these plants failed to thrive, though a few have survived. Mulching of the forest trees has been found successful in reducing the loss of these seedlings due to erosion. Mulching materials are scarce in the area and burlap sacks weighted down with rocks proved less successful than sizable tangles of vines surrounding the trees and weighted with logs or rocks. (PLATE II, FIG. 2). Scattered plantings of grass tufts within the forest tree plantings have also helped to reduce erosion. Application of chicken manure or commercial fertilizer has hastened the establishment

of the grass. Experience has shown, however, that until a complete ground cover is established, sizable accumulations of silt can be expected in the bottoms of the mined-out pits. If saplings are planted in the bottom areas, silting causes the death of a high percentage of these young trees. Planting practices have been adjusted accordingly in recent operations.

Weed control, especially control of vines, remains a major problem in plantation management in the Reynolds area. Only constant attention in the first few years of growth will prevent the vines from either strangling or contorting the young trees. *Ipomoea cathartica* and *Ipomoea tiliacea* are the major pests, along with several others of lesser importance. Hand labor originally was directed at cutting these vines away from the young trees, but this technique had little lasting effect. More recently, grubbing all the plants from the area at the base of the tree with a broad-bladed hoe has been more effective. Clearing the area of vines has also supplied the mulching material to be applied in newer forest plantings where a ground cover of vegetation has not been established.

These initial years of mining operations in Jamaica have been marked with admirable cooperation between the government of Jamaica, through its various departments, and the mining companies. The strip-mining technique and its implications are new to the islands of the West Indies. Certainly the program of land reclamation following mining operations is new to the tropics of the Western Hemisphere. Much has been learned in the past four years and although not all problems are solved, the direction of cooperation and intent is encouraging. The improvement of existing agricultural lands, the rehabilitation of mined-out pits, the introduction of new capital and additional employment, the added source of local and governmental income and the demonstrations of new techniques along with the exchange of knowledge have been the subject of mutual concern and mutual welfare to the government, the people and the mining companies. Agriculture and forestry have taken steps forward in meeting the problems presented and it is hoped the information gained will be shared in furthering the knowledge and the welfare of the West Indies.

(*To be continued*)

Arnold Arboretum
and
The Institute of Jamaica

EXPLANATION OF PLATES *

Plate I, Figure 1. View of the escarpment and area of mining operations of Reynolds Jamaica Mines near Lydford P. O. in St. Ann Parish. Pasture area in foreground is on a limestone outcrop. The intermediate area represents a deeper body of ore. Areas in view between wooded limestone outcrops have been mined out and replanted. Arrows indicate areas of transects. Lower arrow shows forest of Transect #1 and upper arrow, forest of Transect #2.

* Plates I–V: Reynolds Jamaica Mines area in St. Ann. Plates VI–IX: Kaiser Bauxite Company in St. Elizabeth.

PLATE I, FIGURE 2. Mining operations in St. Elizabeth. A cockpit-type depression between two limestone hills containing accumulations of bauxite ore being mined by power shovel.

PLATE II, FIGURE 1. A mined-out ore body now preserved as a control area. Six months after mining operation ceased only herbaceous plants and young shrubs were present. Two and one-half years later, at the time of this picture, shrubs dominate the herbaceous invaders and five species of trees, starting from seed, have grown into conspicuous plants.

PLATE II, FIGURE 2. A mined-out ore body adjacent to control pit. The need for a covering vegetation to control erosion is evident. Young avocado plants are mulched with vines and debris cut from adjacent fields. For a comparison showing the growth one year later, see PLATE IV, FIGURE 1.

PLATE III, FIGURE 1. *Zanthoxylum martinicense* in control pit. This specimen first recorded as a six-inch spontaneous seedling and then as a sapling three feet tall nine months prior to the date of this picture.

PLATE III, FIGURE 2. Woody plants in the control pit representing spontaneous invaders grown from seed. *Ochroma pyramidale*, *Zanthoxylum martinicense*, *Cecropia palmata*, *Terminalia latifolia* and *Petitia domingensis* are all represented in this group. Growth to heights of twelve (*Zanthoxylum*) and fifteen feet (*Ochroma*) occurred in the period of two years' observation.

PLATE IV, FIGURE 1. An avocado tree which bore several fruits two years after being planted as a sapling (see PLATE II, FIGURE 2) on a mined-out bauxite pit. Para grass and wynne grass have been planted on the slopes of this pit and were fertilized with an initial application of chicken manure. The grasses now appear to have become established and are effectively checking the erosion on the slopes.

PLATE IV, FIGURE 2. Mahoe (*Hibiscus elatus*) planted on a mined-out pit. The largest specimens shown were planted as saplings about three feet tall two years previously. The plants died back to six inches in height (see PLATE VIII, FIGURE 1) before the root system became established. The plants were pruned to a single stem and the trees illustrated developed to a height of eighteen feet with trunk diameters of six inches in two years. The smaller trees shown in the picture indicate that growth is slow until a vigorous root development is made. Several trees show trunks covered with herbaceous and semi-woody vines. The ground cover is natural weed vegetation dominated by *Borreria verticillata* and *Wedelia gracilis*, with *Mimosa pudica*, *Desmodium canum* and *Bidens cynapifolia* also abundant.

PLATE V, FIGURE 1. Pasture area in St. Ann prior to mining. Shrub invasion of one section of this pasture is conspicuous in the foreground.

PLATE V, FIGURE 2. The same area two years later. Bauxite ore has been removed. The pit surfaces were contoured and the overburden replaced. The rehabilitated pit was then planted to para grass and fertilized with chicken manure to establish the grass. The relative productivity of the area has been increased about five times in terms of quality pasture with a slight increase in pasture acreage in this tract.

PLATE VI, FIGURE 1. Area of Kaiser Bauxite Company mining operation in St. Elizabeth parish. Photograph shows the dominance of shrubby vegetation on a pasture area. Two years earlier this pasture had been open and was easily grazed by cattle. Shrubs are *Solanum* spp., *Haematoxylon campechianum* and

Latana camara. Two forested limestone outcrops are visible in the background. The area between the forests of broad-leaved species comprises a dense stand of logwood (*Haematoxylon campechianum*) on limestone with recent development of broad-leaved species not evident in the photograph. TRANSECT #8 was made in the forested hill on the right. QUADRAT #6 was made in the overgrown pasture beyond the right-hand side of the picture.

PLATE VI, FIGURE 2. An area near New Buildings in St. Elizabeth being prepared for mining. The overburden has been removed by bulldozers and is piled at the left of the picture. A dragline shovel in the center at the rear is used to remove the ore.

PLATE VII, FIGURE 1. An area comparable to that of PLATE VI, FIGURE 2 following planting of forage grasses. Mining has been completed. The deeper pits have been partially filled and the slopes eased. Contours have been established on the slopes and pangola grass has been planted.

PLATE VII, FIGURE 2. A mined-out pit replanted to guinea grass. This stand is one year old. Commercial fertilizer was used to establish the grass.

PLATE VIII, FIGURE 1. An example of "die-back" in young mahoe plants. A three-foot sapling has died back to six inches and three lateral buds have started to develop into shoots. Die-back has been reduced by better soil preparation and by more careful attention to planting during the rainy periods.

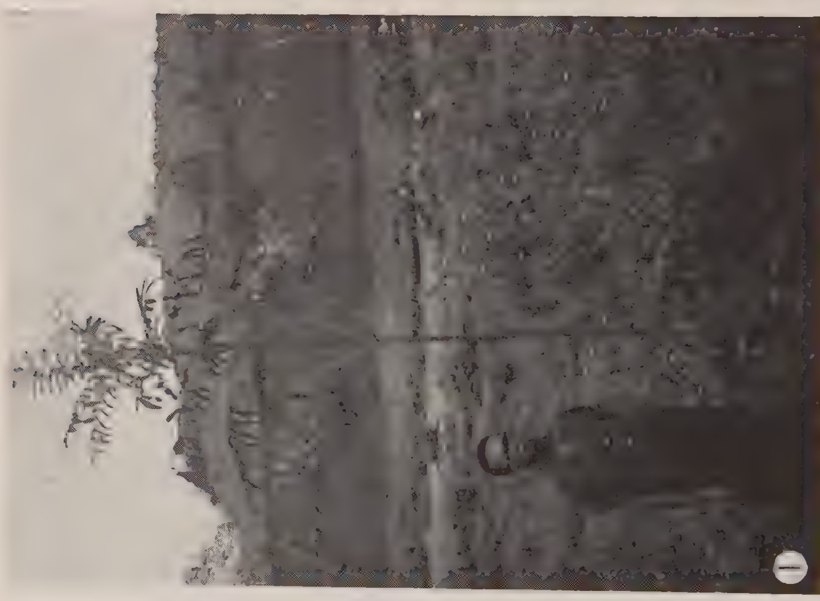
PLATE VIII, FIGURE 2. The type of mahoe plant which develops from saplings having suffered from die-back. Such a tree is of no commercial value. Proper pruning is essential for plants which suffer die-back if a single-trunked, marketable timber tree is to be produced.

PLATE IX, FIGURE 1. A mature stand of logwood (*Haematoxylon campechianum*) on bauxite soils in St. Elizabeth. The commercial market for logwood has been small in the last decade, but limited supplies can still be sold. Few broad-leaved species are found in logwood forests on bauxite soils in contrast with the dominance of broad-leaved species over logwood on limestone outcrops.

PLATE IX, FIGURE 2. Forest planting on a mined-out pit in St. Elizabeth. The photograph was taken three years after planting saplings in the area. Plants of *Cassia siamea* on either side of Mr. Proctor are twenty feet tall with trunk diameters of five inches at breast height. The mahoe shown at the sides were fifteen feet tall and were in flower. The mahogany trees in this mixed planting were seven feet tall and one is shown at the right side of the picture. Proper pruning practices have been essential in this area where both *Cassia siamea* and *Hibiscus elatus* plants tended to branch freely near the base. The plants illustrated are the best specimens in this rehabilitated pit area and cannot be regarded as average for the area.

Howard & Proctor, Vegetation on Bauxitic Soils

Howard & Proctor, Vegetation on Bauxitic Soils



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Howard & Proctor, Vegetation on Bauxitic Soils

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

Grady L. Webster

With one plate

Subgenus II. **Kirganelia** (Juss.) Webster, Jour. Arnold Arb. **37**: 344. 1956.

Kirganelia Juss. Gen. Pl. 387. 1789.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea **32**: 11. 1863; DC. Prodr. **15**(2): 341. 1866.

Trees, shrubs, or herbs with phyllanthoid branching; monoecious or dioecious. Male flower: calyx-lobes 5 or 6; disk of 5 or 6 segments; stamens 5 or 6, free or rarely united by the filaments; anthers dehiscing vertically or horizontally; pollen grains more or less globose, colporate. Female flower: calyx-lobes 5 or 6; disk usually as in male; ovary of 3–12 carpels; styles mostly bifid, sometimes entire, often thickened and fleshy. Fruit capsular or baccate; seeds trigonous.

This subgenus, typified by sect. *Anisonema*, comprises about 35 species in several closely related sections. None is native to the New World, and most of the species are restricted to Africa and the Mascarene islands, although they also occur in India, China, Japan, Malaysia, and Australia. Subgenus *Kirganelia* includes not only some of the most primitive of the species with phyllanthoid branching but also a number of highly specialized herbaceous species (in sect. *Floribundi*) which form a transition to the herbaceous representatives of sect. *Phyllanthus*. A significant indication of the relative primitiveness of this subgenus is the great floral variability. In the West Indies subgenus *Kirganelia* is represented by two very different species belonging to two different sections.

KEY TO THE SECTIONS

Fruit capsular; stamens 5, filaments free .... 2. **Floribundi**
Fruit baccate; filaments connate in two groups .... 3. **Anisonema**

Sect. 2. **Floribundi** Pax & Hoffm. Pflanzenw. Afr. 3(2): 22. 1921.

Trees, shrubs, or herbs with phyllanthoid branching; leaves (in ours) membranous, not over 2 cm. long. Monoecious or dioecious, flowers in abbreviated unisexual or bisexual axillary cymules. Male flower: calyx-lobes 5, small, uninerved; disk of 5 discrete segments; stamens 5, filaments free; anthers dehiscing vertically or horizontally; pollen grains subglobose, 4-colporate (in *P. tenellus*), finely reticulate. Female flower: pedicel long

* Continued from volume XXXVII, p. 359.

and capillary; disk cupulate; ovary of 3 carpels, smooth; styles free or united beneath, bifid, the style-branches slender or dilated. Capsule oblate, the valves membranous and veiny; seeds trigonous, smooth or rugulose.

TYPE SPECIES: *Phyllanthus floribundus* Muell. Arg. [= *P. muelleranus* Exell].

This exclusively Old World section of perhaps 10 to 15 species is best developed in Africa; only one species, *P. tenellus* Roxb., has become naturalized in America. The group as here defined has a different circumscription from that of Pax and Hoffmann. They included in sect. *Floribundi* those species previously classified in sect. *Menarda* which had fascicles of inflorescences at the nodes. Consequently, they retained *P. tenellus* and its relatives, which lack fascicled inflorescences, in sect. *Menarda*. Unfortunately, however, even the emended sect. *Menarda* of Pax and Hoffmann contains discordant elements. The type species, *P. cryptophilus* (A. Juss.) Muell. Arg., contrasts with all of the other species by virtue of its non-phyllanthoid branching and opposite leaves of peculiar texture. In the present circumscription, therefore, sect. *Menarda* is restricted to *P. cryptophilus* and a few other species of Madagascar, while all of the other species placed in the group by Mueller and by Pax are removed to sect. *Floribundi*. The latter, as thus constituted, is polymorphic and perhaps could be further divided, but any additional change in its definition must await careful study of the African species.

The description of the section is based primarily on the single species in the West Indies, *P. tenellus*, and therefore cannot be regarded as authoritative for the entire section. The relationships of sect. *Floribundi* are perhaps closest to sect. *Chorisandra* (Wight) Muell. Arg. The type species of the latter group, *P. pinnatus*,[11] agrees in having a crustaceous capsule, slender bifid styles, and free stamens (though 6 in number instead of 5). However, the seeds of *P. pinnatus* are very different, being hollowed out at the hilum. It is possible that further study may result in the merging of the two sections. On the other hand, sect. *Floribundi* is doubtless rather closely related to sect. *Anisonema*. Although the West Indian representatives of both groups are very easy to distinguish, there are species in Africa and Madagascar which seem to defy sectional limits; and future revision in the boundaries of these two groups may perhaps be required, although they are so distinctive on the whole that there would appear to be little advantage in merging them.

4. **Phyllanthus tenellus** Roxb. Fl. Ind. [ed. 2] 3: 668. 1832; Muell. Arg. in DC. Prodr. **15**(2): 337. 1866; Hook. f. in Hook. Icon. 1569. 1887. (TEXT-FIG. 6; PLATE I, *fig.* 3).

Phyllanthus corcovadensis Muell. Arg. Fl. Bras. **11**(2): 30, *pl. 6, fig. 2.* 1873.
Diasperus tenellus (Roxb. "em.") O. Ktze. Rev. Gen. **2**: 601. 1891.

[11] **Phyllanthus pinnatus** (Wight) comb. nov.; *Chorisandra pinnata* Wight, Icon. Pl. Ind. Or. **6**: 13, *pl. 1994.* 1853; *Phyllanthus wightianus* Muell. Arg.

Phyllanthus minor Fawc. & Rend. Jour. Bot. **57**: 65–66. 1919.
Phyllanthus nummulariaefolius sensu Croizat, Torreya **42**: 14. 1942; non *P. nummulariaefolius* Poir.

Erect annual herb, typically with a single main (primary) stem c. 2 — 5 dm. high, 1.5 — 2 mm. thick, olivaceous or stramineous, smooth, terete or roundly angled, sometimes channelled; internodes mostly 10 — 35 mm. long. Cataphylls: stipules lanceolate, 0.7 — 1 mm. long, 0.2 — 0.3 mm. broad, acuminate, not auriculate, entire, olivaceous or reddish with rather narrow scarious margins; blade linear-lanceolate, 0.6 — 0.9 mm. long, attenuate-acuminate, similarly colored. Penultimate branches well developed in vigorous individuals (becoming up to 2 dm. long) or quite suppressed in smaller plants. Deciduous branchlets ascending, mostly 5 — 15 cm. long, 0.25 — 0.5 mm. thick, olivaceous, smooth or scabridulous, somewhat angled, with mostly 10 — 25 leaves; first internode (5–) 8 — 15 (–25) mm. long, median internodes c. 3 — 6 mm. long. Leaves: stipules lanceolate, 0.7 — 1.1 mm. long, acuminate, not auriculate, entire, olivaceous or reddish with white scarious margins. Petiole 0.5 — 0.8 mm. long. Leaf-blades membranous, smooth on both sides, mostly broadly elliptic to obovate, (6–) 10 — 20 (–24) mm. long, (4–) 5 — 9 (–11) mm. broad, acute or obtuse at the tip, acute to rounded at the base; above bright or dark green with the midrib and arching laterals (5 — 8 on a side) slightly raised; beneath pallid, the midrib raised, the laterals forming with the tertiary veinlets a fine reticulum; margins smooth.

Monoecious; all axils of deciduous branchlets usually floriferous. Proximal axils bisexual, the 1 or 2 female flowers beneath, the 2 or 3 male flowers above; distalmost cymules usually reduced to a single female flower.

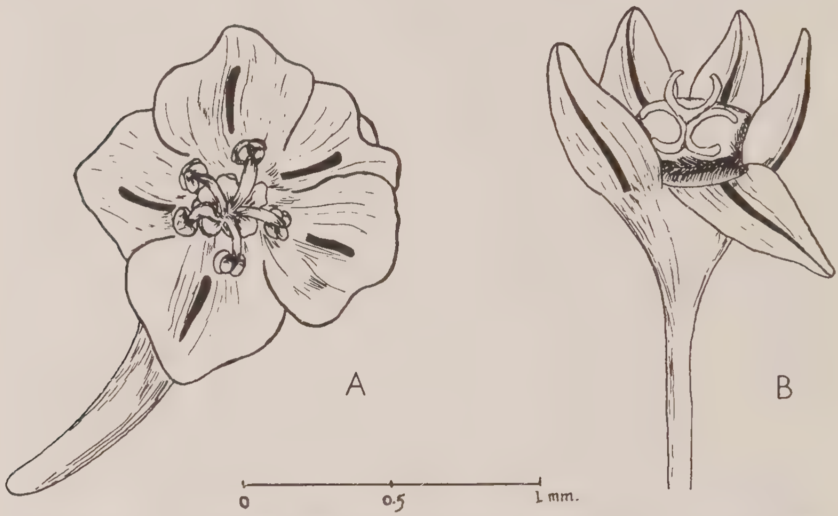
Male flower: Pedicel filiform, 0.5 — 1.5 mm. long. Calyx-lobes 5, imbricate at anthesis, subequal, broadly elliptic or obovate, c. 0.4 — 0.6 (–0.7) mm. long, 0.5 — 0.7 (–0.8) mm. broad, acute to rounded at the tip, entire, membranous, whitish except for the narrow green unbranched midrib. Disk-segments 5, broadly cuneate, thin, entire, c. 0.2 mm. across. Stamens 5, alternate with the disk-segments; filaments free, filiform, c. 0.2 — 0.3 mm. long, bent near the top; anthers reniform, 0.15 — 0.25 mm. broad, the long axis almost or quite horizontal; anther-sacs divergent, the slits confluent near the apex of the anther; pollen grains 17.5 — 19 μ in diameter, 4-colporate, the colpi not meeting at the poles.

Female flower: Pedicel capillary and flexuous, (2.5–) 3 — 5 (–7) mm. long, olivaceous (or reddish below), smooth and terete, dilated into a cylindrical pulvinus at the base and often bent at the pulvinar apex. Calyx-lobes 5, spreading at anthesis, triangular-ovate, 0.6 — 0.8 mm. long, 0.3 — 0.5 mm. broad, narrowed to an acute tip (in fruit reflexed, elliptic or oblong, and obtuse), entire, membranous, whitish except for the narrow green unbranched midrib. Disk patelliform, fleshy but thin, the margins undulate. Styles free, horizontally appressed, spreading, c. 0.25

mm. long, very slender, bifid to ⅔ parted, the branches divaricately spreading, the tips subcapitate.

Capsule oblate, rounded-trigonous, c. 1 mm. high, 1.7 — 1.9 mm. in diameter, greenish, obscurely reticulate-veiny. Seeds trigonous, c. 0.9 mm. long, 0.7 — 0.75 mm. radially and tangentially, light brown, densely pebbled on all sides with rounded processes; hilum linear-oblong.

Collected May through December, but perhaps flowering throughout the year where conditions are favorable.



TEXT-FIG. 6. *Phyllanthus tenellus* Roxb. (*Harris 12204*[GH]). A, male flower; B, female flower.

TYPE: Botanic Gardens, Calcutta, *Wallich 7892A ex p.* (K, HOLOTYPE). According to Roxburgh, the species was introduced from Mauritius in 1802 by Captain Tennant. However, Baker (Fl. Maur. 310. 1873) was unable to find a single Mauritian specimen of the plant. Since it appears improbable that so aggressive a weed as *P. tenellus* could have been overlooked by visitors to that island, the species was most likely collected in one of the other Mascarene islands. De Cordemoy (Fl. Reunion 346. 1895), for instance, has recorded it as very common everywhere in Reunion.

DISTRIBUTION: the typical var. *tenellus* (var. *roxburghii* of Mueller), native to the Mascarene islands, has been introduced into the southeastern United States, the West Indies, Brazil, and doubtless other areas of the New World.

JAMAICA. St. ANN: Mt. Diablo, road to Hollymount, *Webster & Wilson 5016* (A, JAM, MICH). CLARENDON: 0.5 mile NW of Kupuis, *Proctor 10331* (GH). ST. ANDREW: Hope Grounds, in shady places, alt. 700 ft., *Harris 12123* (GH, NY, US), *12157* (NY, US), *12208* (GH, JAM, MT, NY, US; *P. minor* based on all three Harris collections).

LESSER ANTILLES. GUADELOUPE: Camp-Jacob, Choisy, Bagatelle, *Duss 2442, 3557* (NY); Montebello, *Questel 440* (US); between Goyave and Petit Bourg, Bailly, *Rodriguez 4390, 3935bis* (P). DOMINICA: Sylvania Estate, cleared forest land, *Hodge 573* (NY). MARTINIQUE: Morne-Rouge, Carbet, Fonds St. Denis, *Duss 47a* (NY, US); 1847, *Hahn 374* (A, P); environs St. Pierre, *Hahn 585* (G); St. Pierre, *Steinheil 24 ex p.* (P, mixed with *P. amarus*). GRENADA: under nutmegs, Grenville Vale, St. George Parish, *Hunnewell 19476* (GH).

Croizat (loc. cit.) has followed the example of Leandri (Not. Syst. 7: 168–169. 1939) in reducing *P. tenellus* to a synonym of *P. nummulariaefolius* Poir. As Leandri remarks, leaf size and pedicel length are excessively variable in this species-group, and the distinguishing characters proposed by Mueller are not convincing. Nevertheless, after examination of the holotype of *P. nummulariaefolius* (Herb. Lam., P) and of some Madagascar specimens cited by Leandri (*Humbert 5848, 6122*; A), I believe that these specimens represent a species closely allied to but distinct from *P. tenellus*. The calyx-lobes of the male flower of *P. nummulariaefolius* are about 1 mm. long, or almost twice the length of those of *P. tenellus;* and the pedicel of the male flower is about 3 — 6 mm. long in the former species, while in our West Indian plants it is never over 1.5 mm. in length. The leaf-shape also appears to be somewhat different in the two species, the blade of *P. nummulariaefolius* being rhombic- or suborbicular-obovate and rather abruptly contracted to a point, while that of *P. tenellus* is obovate and smoothly obtuse or rounded at the tip. Fawcett and Rendle were correct in noting the differences between the Jamaican plant and *P. nummulariaefolius*, but did not realize that the former was conspecific with *P. tenellus*.

As Leandri has observed (in lit.), the species of the complex to which *P. nummulariaefolius* and *P. tenellus* belong are at present so poorly defined that a careful monographic revision of them will be necessary before there can be any confidence with regard to species delimitation. The status of the six additional varieties of *P. tenellus* described by Mueller, as well as such closely allied species as *P. capillaris* Schum., must therefore be regarded as provisional.

The earliest record of *P. tenellus* from the West Indies is apparently the collection made on Martinique in 1839 by Steinheil. Judging from its rapid spread over Florida and Georgia within about twenty years of its introduction into the United States, it probably dispersed rapidly over the Lesser Antilles once given a foothold there. Its present naturalized area in the West Indies is strikingly parallel to that of another Old World congener, *P. urinaria*; both are widespread in Jamaica and the Lesser Antilles but have failed to become established on Cuba, Hispaniola, or Puerto Rico. The reasons for this are not entirely clear, for there are plenty of mesophytic habitats in the latter group of islands which would be attractive to the two species. The absence of *P. tenellus* from these islands is particularly surprising in view of the aggressively weedy nature of the plant; as Croizat remarks, it will quickly overrun a greenhouse if given a chance.

This "aggressive" nature of *P. tenellus* is largely due to the rapidity of growth and reproductive maturation of the plant. A seedling when only a few centimeters high is already producing explosively dehiscent capsules, and deciduous branchlets which have only two or three leaves unrolled will already have a completely developed fruit.

Phylogenetically *P. tenellus* is of considerable interest, because it and its allies appear to represent the link connecting the shrubby species of sect. *Floribundi* with the herbaceous species of sect. *Phyllanthus*. In its usual growth habit it agrees with some of the latter so closely that it can easily be confused with them. However, when grown in the greenhouse *P. tenellus* betrays its less specialized nature, for it may persist three years or more, become definitely shrubby at the base, and branch many times above. Indeed, Roxburgh reported that his original plant in the gardens at Calcutta grew to be a shrub 3.5 feet high. In contrast, the annual herbaceous species of sect. *Phyllanthus* such as *P. amarus* live only about a year or less even when pampered in the greenhouse.

Although the general aspect of *P. tenellus* is that of many species of sect. *Phyllanthus*, there is no reason why it should be confused with them. The long pendent capillary fruiting pedicels of *P. tenellus* are diagnostic, and of course no other herbaceous West Indian species has male flowers with five free stamens.

Sect. 3. **Anisonema** (A. Juss.) Griseb. Fl. Br. W. Ind. 34. 1859.

Kirganelia Juss. Gen. Pl. 387. 1789.
Anisonema A. Juss. Euphorb. Tent. 19, *pl. 4, fig. 11.* 1824.
Kirganelia sect. *Anisonema* (A. Juss.) Baill. Etud. Gen. Euphorb. 613–614. 1858.
Kirganelia sect. *Anisonemopsis* Baill. op. cit. 614.
Kirganelia sect. *Eukirganelia* Baill. ibid.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea 32: 11, 1863; DC. Prodr. **15**(2): 341. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Kirganelia* (Juss.) O. Ktze. in Post & Kuntze, Lexicon 434. 1904.

Shrubs or small trees with the habit of *Breynia;* leaves chartaceous with rather conspicuous venation. Monoecious; flowers long-pedicelled, in bisexual cymules, the female flowers one or few, the males more numerous. Male flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete segments; stamens 5, unequal, in two sets: the inner connate with long filaments, the outer discrete with shorter filaments, filaments all free in some extralimital species fide Mueller; anthers extrorse, dehiscing longitudinally, the anther-sacs not confluent; pollen grains globose, tricolporate, finely reticulate. Female flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete or paired contiguous segments; ovary smooth, of 3 — 12 carpels; styles more or less bifid, often thickened and fleshy, more or less connivent. Fruit capsular or baccate; seeds trigonous.

TYPE SPECIES: *Phyllanthus reticulatus* Poir.

This section of about 10 Old World species is best distinguished by the curious androecium of five stamens unequally united into two sets. *Anisonema* and *Kirganelia* were distinguished by A. Jussieu (as genera) and by Baillon (as sections) on the basis of the number of locules in the ovary. However, the type species of the two groups, *P. reticulatus* Poir. and *P. casticum* Willem., agree in having the characteristic androecium, and Mueller was quite justified in combining them. Possibly he did not go far enough, for some of the species he included in his sect. *Kirganelia*, such as *P. physocarpus*, could as easily be placed in his sect. *Menarda* (i.e., sect. *Floribundi*).

The taxonomic difficulties attendant with sectional limits here are aggravated by the nomenclatural vagaries of typification. Mueller (DC. Prodr. **15**(2): 341. 1866) and Pax and Hoffmann (Naturl. Pflanzenfam. **19c**: 62. 1931) applied the epithet *Kirganelia* to the present section. It is true that *Kirganelia* is the oldest generic name, but as a sectional name in *Phyllanthus* it must yield priority to *Anisonema*. This, as it turns out, is fortunate, because the type species of *Kirganelia* (*P. casticum*) has such a broad latitude of variation that among its own subspecies it nearly bridges the gap with sect. *Flueggeopsis*. All these nomenclatural difficulties are symptoms of an unstable taxonomy. When a monographic study can be made of subg. *Kirganelia*, it is likely that several of these closely related sections will be combined.

In the West Indies sect. *Anisonema* is represented only by a single introduced species.

5. **Phyllanthus reticulatus** Poir. Enc. Method. **5**: 298. 1804 (as *P. reticulata*); Muell. Arg. in DC. Prodr. **15**(2): 345. 1866. (TEXT-FIG. 7).

Phyllanthus jamaicensis Griseb. Fl. Br. W. Ind. 34. 1859 (for the remainder of the complicated synonymy see Mueller loc. cit.).

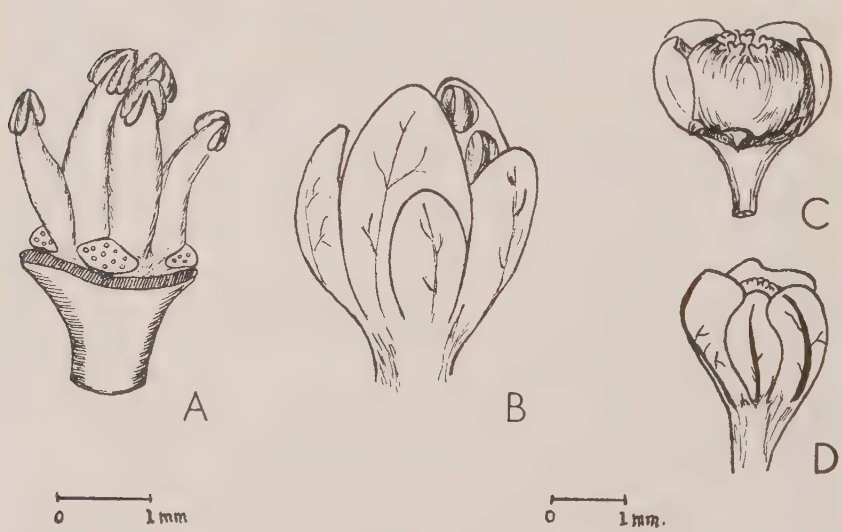
A much-branching shrub or small bushy tree up to 4 m. high; branches of current year smooth and glabrous, somewhat angled, dark brown, 2 — 3 mm. thick, with internodes mostly 1 — 2 cm. long. Cataphylls: stipules triangular, (1.2–) 1.5 — 1.7 mm. long, mostly 1 — 1.4 mm. broad, acuminate, truncate at the base, subcarnose, dark blackish brown, margins ciliate; blade lanceolate, (1.1–) 1.3 — 1.7 mm. long, 0.4 — 0.9 mm. broad, acuminate, similar in texture, ciliate. Deciduous branchlets steeply ascending, (8.5–) 10 — 20 (–25) cm. long, 0.5 — 1 mm. thick, dark brown, somewhat angled, quite smooth, with (10–) 13 — 16 (–25) leaves; internodes mostly 7 — 13 mm. long. Leaves: stipules lanceolate, (0.8–) 1 — 1.4 (–1.6) mm. long, 0.5 — 0.7 mm. broad, acuminate, truncate at the base, margins ciliate, olivaceous turning more or less dark brownish, rather scarious. Petioles smooth, plano-convex, 1.5 — 2.5 mm. long. Leaf-blades chartaceous, smooth on both surfaces, elliptic, (13–) 15 — 25 (–32) mm. long, (9–) 10 — 15 mm. broad, obtuse or rounded at the tip, cuneate at the base; midrib and laterals (5 — 7 on a side) raised and conspicuous

particularly beneath, where they form with the tertiaries a conspicuous reticulum; margins not thickened, more or less plane.

Monoecious; most deciduous branchlets floriferous; first 1 or 2 (rarely more) proximal nodes barren, succeeding ones with bisexual cymules; female flower solitary or sometimes paired in each cymule, male flowers up to 8.

Male flower: pedicel capillary, 5 — 10 mm. long. Calyx-lobes 5 or 6, unequal, imbricate in 2 or 3 series, c. 2 — 2.5 mm. long, the outer oblong or obovate, rounded at the tip and c. 0.7 — 1.2 mm. broad, the inner nearly orbicular, subtruncate at the tip and c. 1.3 — 1.8 mm. broad; lobes of both series entire, with simple or sparsely branched midrib, somewhat thickened adaxially at the base; margins thin and scarious. Disk-segments 5, broadly ovate or reniform, thin, subcarnose, erect, entire, foveolate, 0.35 — 0.5 mm. across. Stamens 5, erect, in two sets: three with longer filaments (0.7 — 1.3 mm. long) coherent in a central column, two with shorter filaments (0.3 — 0.8 mm. long) free and displaced to the sides — or vice versa (i.e., two stamens central and coherent with three shorter ones peripheral and more or less free); filaments fusiform, often conspicuously thicker than the anthers, 0.25 — 0.5 (–0.6) mm. broad. Anthers erect, triangular, c. 0.3 — 0.5 mm. long and broad; anther-sacs divergent, dehiscing longitudinally, discrete, the slits apically contiguous but not confluent; pollen grains c. 14 — 17 μ in diameter, tricolporate, colpi conspicuously bordered and meeting at the poles, reticulum rather coarse.

Female flower: pedicel subterete, slender, (4–) 5 — 8 mm. long. Calyx-



TEXT-FIG. 7. *Phyllanthus reticulatus* Poir. (*Webster & Wilson 5237*[A]). A male flower with calyx-lobes removed to show androecium and disk; B, male flower entire; C, female flower with two calyx-lobes removed to show ovary and styles; D, female flower entire (B, C, and D to the same scale).

lobes 5 or 6, erect and closely investing the ovary, unequal, in 2 or 3 series (the innermost segment completely overlapped by the others); the outer oblong-elliptic, c. 1.6 — 1.8 mm. long and 0.9 — 1.2 mm. broad, strongly carinate, midrib simple or sparsely branched; the inner nearly orbicular, c. 1.4 — 1.7 mm. long, 1.2 — 1.5 mm. broad, carinate or plane, the midrib sparingly branched. Disk-segments 5 or 6, often subpaired, oblong or cuneate, somewhat thickened and fleshy, c. 0.3 — 0.4 mm. broad, obscurely foveolate. Ovary oblate-spheroidal, smooth, not perceptibly sulcate; carpels mostly 9 or 10 (in West Indian material); styles c. 0.25 mm. long, bifid, thickened and fleshy, free but inflexing and connivent over the top of the ovary as an irregular furrowed mass of stigmatic tissue.

Mature fruit baccate, globose or oblate, c. 4 — 6 mm. in diameter, shiny black with dark purplish pulp. Seeds trigonous (when in pairs), c. 1.6 — 2 mm. long, blackish, colliculose; hilum shallow, less than 0.5 mm. across.

Flowering and fruiting March to July, and probably later in the year as well.

Type: Herb. Lamarck (P, holotype). The type sheet contains a mixture of *P. reticulatus* and a species of *Breynia*.

Distribution: Widespread in the Old World from West Africa to India, Ceylon, China, Indonesia, the Philippines, and Queensland; introduced into the West Indies.

JAMAICA. common, Oct. 1857, *Wilson* (GOET, holotype of *P. jamaicensis*); donne par Sir W. Hooker, 1845 (P); center and east Jamaica, thickets and river banks, *Velez 3781* (US). St. Thomas: shores of Plantain Garden River, *Harris & Britton 10677* (NY, US), *Webster & Wilson 5237* (A, JAM, MICH); Bath, *Orcutt 2013* (US); fields, Holland Bay, *Britton 4067* (NY).

LESSER ANTILLES. St. Vincent: *Caley* (P); Liberty Lodge, alt. 500 ft., *Eggers 6769* (GOET, P, US); thickets near houses, hills near Kingstown, alt. 800 ft., *H. H. & G. W. Smith 872* (NY).

This introduced Old World plant is readily recognizable by virtue of its peculiar androecium and baccate fruit, and cannot be mistaken for any native West Indian species. Although in its native range *P. reticulatus* is extremely variable, the specimens from the West Indian populations all represent the glabrous form, var. *glaber* of Mueller. Poiret's type specimen is definitely pubescent, but since — as pointed out by J. D. Hooker (Fl. Br. Ind. 5: 288. 1887) — the pubescent and glabrous forms occur indiscriminately together, it does not seem worthwhile to designate the form in the West Indies with a varietal name. *Phyllanthus jamaicensis* Griseb. was described under the mistaken impression that the plant was endemic to Jamaica. However, the specimen collected by Wilson and now in the Herbarium Grisebachianum (GOET) can be matched by many sheets from the Old World, and shows no significant differences.

The only striking peculiarity of the West Indian specimens of *P. reticulatus* appears to be their infertility. Only two fruits were observed on a copiously flowering plant seen in the field at the Plantain Garden River, Jamaica (*Webster & Wilson 5237*), and each of these contained but a single well-developed seed. In contrast, many specimens from the Old World — e.g., *Merrill Species Blancoanae 674* (A) — have numbers of fruits, each of which have 12 — 16 mature seeds.

J. J. Smith (Add. Fl. Arb. Jav. 12: 67. 1910) describes the seeds of a living plant of *P. reticulatus* as greenish, with "testae strato exteriore succoso, strato interiore duro." If the seed-coat of *P. reticulatus* is actually fleshy, this would be an extremely interesting indication of a close relationship between this plant and species of *Glochidion* and *Breynia*. However, judging from the seeds of *Webster & Wilson 5237* and *Merrill 674*, the seed-coat could at most be called slightly fleshy. The outer seed-coat is scarcely thicker than the inner and certainly appears no different from that of many typical species of *Phyllanthus*. Furthermore, since there is no hilar indentation in *P. reticulatus* and the embryo is straight, it does not appear that this species represents a very close approach to the seed structure of *Glochidion*.

Subgenus III. **Cicca** (L.) Webster, Jour. Arnold Arb. 37: 344. 1956.

Cicca L. Mant. 17. 1767.

Trees or rarely shrubs with phyllanthoid branching. Monoecious or dioecious, inflorescences commonly fascicled or cauliflorous. Male flower: calyx-lobes 4 — 6; disk of 4 — 6 segments or absent; stamens 3 or 4 (rarely 2 or 5), filaments free; anthers dehiscing more or less vertically; pollen grains 3-colporate. Female flower: calyx-lobes 4 — 6; disk cupuliform or absent; ovary of 2 — 4 carpels; styles bifid, free or shortly connate at the base. Fruit indehiscent, woody or drupaceous; seeds 1 or 2 in each fertile locule.

This subgenus contains some of the most distinctive groups in the genus, and it is not surprising that at times sects. *Cicca*, *Aporosella*, and *Emblica* have been recognized as generically distinct from *Phyllanthus*. The accumulation of further evidence from such fields as wood anatomy and cytology may possibly justify the maintenance of one or more of these groups as an independent genus. However, at the present time they seem best regarded as divergent sections of *Phyllanthus*, especially since sect. *Ciccopsis* would appear to at least partially bridge the gap between sect. *Cicca* and typical representatives of sect. *Kirganelia*. It should also be pointed out here that the inclusion of sect. *Emblica* in the present subgenus is quite possibly contrary to natural relationship, and is justified in this West Indian study on the grounds of convenience.[12] With the exception of sect. *Emblica*, the species of subg. *Cicca* are all native to the New World.

[12] The description of the subgenus applies only to the American representatives and does not refer to the special features of sect. *Emblica*.

KEY TO THE SECTIONS

1. Calyx-lobes 6; male flower with 3 stamens, the filaments free; leaves elliptic, obtuse or rounded at the tip. . . . . 4. **Ciccopsis**
1. Calyx-lobes 4 or if 6 then filaments of stamens united; leaves otherwise.
    2. Fruit indehiscent; calyx-lobes usually 4; leaves elliptic to ovate; female disk small or absent.
        3. Fruit drupaceous; monoecious (in West Indies); disk present; staminodes often present . . . . 5. **Cicca**
        3. Fruit pithy; dioecious; disk and staminodes absent. . . . . 6. **Aporosella**
    2. Fruit fleshy but at length dehiscent; calyx-lobes 6; leaves linear-oblong; female disk urceolate. . . . . 7. **Emblica**

Sect. 4. **Ciccopsis** Webster, Contr. Gray Herb. **176**: 57. 1955.

Shrubs or trees with phyllanthoid branching; cataphylls persistent; branchlets compressed, angled, often borne on spur-shoots; leaves with persistent stipules, corrugate petioles, chartaceous blades; monoecious, inflorescence semi-cauliflorous, the floriferous branchlets more or less fascicled on short spurs. Male flower: calyx-lobes 6, reflexed; disk-segments 6; stamens 3, free, the filaments erect; anthers deflexed at connective; pollen grains tricolporate, angular-aperturate. Female flower: calyx-lobes 6; disk 3-angled; ovary of 3 carpels; styles free, horizontal, bifid. Fruit and seeds unknown.

Type species: *Phyllanthus pseudocicca* Griseb.

This monotypic section is represented only by the type species, which is endemic to a relatively small area in eastern Cuba. Its relationships are somewhat dubious at present because of the doubt as to the nature of the fruit. However, there is little doubt that it is fairly closely related to sect. *Cicca*, if indeed that group is not its nearest ally. The pollen grains of *Cicca* are rather similar, and its cauliflorous condition could be rather easily derived from the semi-cauliflorous behavior of *Ciccopsis*. On the other hand, various African species in subg. *Kirganelia* — in particular *P. physocarpus* Muell. Arg. — have a suggestive general resemblance to *P. pseudocicca* in both floral and vegetative morphology. It is quite possible that sect. *Ciccopsis*, when better understood, may prove to represent the closest approach to a connecting link between subg. *Kirganelia* and subg. *Cicca*.

Section *Ciccopsis* is of further phylogenetic interest because of its apparent relationship to sect. *Omphacodes* (subg. *Xylophylla*). Indeed *P. pseudocicca* and the type species of that section, *P. subcarnosus*, are so strikingly similar in leaf venation and details of floral morphology that a fairly close degree of affinity between them appears highly probable, even though they are widely separated in the linear arrangement of taxa. The somewhat fleshy fruit and the ecological requirements of *P. subcarnosus* further suggest a general relationship to subg. *Cicca*. In fact, if it were not

for their areolate pollen grains, the two species of sect. *Omphacodes* could just as well be put adjacent to sect. *Ciccopsis* in the present arrangement.

6. **Phyllanthus pseudocicca** Griseb. Goett. Nachr. **1865**(7): 166. 1865; Muell. Arg. in DC. Prodr. **15**(2): 384. 1866.
(PLATE XV, *figs. A–C*).

Diasperus pseudocicca (Griseb.) O. Ktze. Rev. Gen. **2**: 600. 1891.
Phyllanthus brevistipulus Urb. Symb. Ant. **9**: 183. 1924.
Phyllanthus punctulatus Urb. ibid. 184.

A glabrous shrub (Ekman) or slender tree to c. 10 m. high (Wright); branches of previous year 3 — 4 mm. thick, with smooth or furrowed greyish bark, old nodes with spur-shoots c. 0.5 — 2 cm. long, 1.5 — 2 mm. thick, smooth or in age roughened with the cataphyll bases. Cataphylls dark brown, indurate, persistent, not reflexed: stipules broadly triangular, c. 1 mm. long and broad, blunt, typically entire, fused at the base into a massive scale; blades lanceolate, inconspicuous, c. 0.5 mm. long or less. Branchlets in part scattered along branches of current year, in part clustered on spur-like branches from the axils of nodes on old wood (i.e., on branches of previous years), 3 — 10 cm. long, 0.5 — 1 mm. thick, somewhat compressed, angled, stramineous, slightly shiny, with 5 — 9 leaves; first internode (5–) 10 — 17 mm. long, median internodes (5–) 7 — 10 (–15) mm. long. Leaves: stipules appressed, persistent, triangular, 0.5 — 1 mm. long and about as broad, blunt-tipped, dark reddish-brown, entire. Petiole (2.5–) 3 — 4 mm. long, stramineous, flattened adaxially, transversely corrugate-lamellate. Leaf blades chartaceous, plane, elliptic or ovate, 2.5 — 5 (–6.5) cm. long, 1.5 — 3 (–4) cm. broad, obtuse or rounded at the tip, mostly obtuse at the base; above olivaceous or brownish (when dried), somewhat shiny, midrib plane or incised, laterals slightly raised, subconspicuous; beneath greyish-green (puncticulate with whitish waxy atoms) or yellowish, the midrib and laterals (4 or 5 on a side) conspicuously raised, anastomosing to form a prominent reticulum; margins thickened, plane or reflexed.

Monoecious (rarely dioecious?); floriferous branchlets sometimes nearly or quite aphyllous (the leaves reduced to cataphylls) but usually with only the proximal 2 — 4 leaves reduced and subtending male cymules, the distal leaves typical and subtending bisexual cymules of one female and several male flowers; occasional branchlets producing only male flowers.

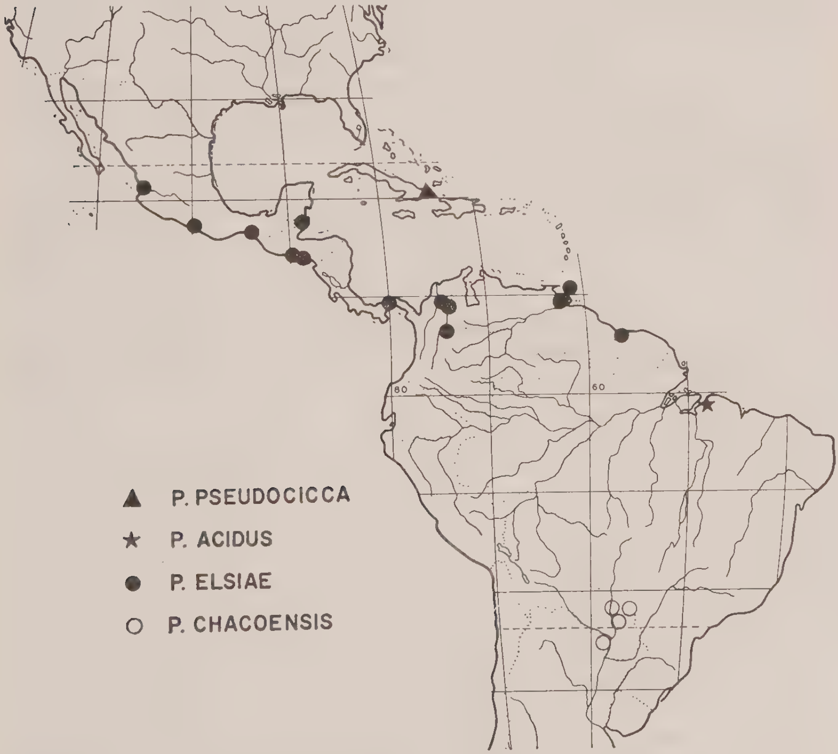
Male flower: pedicel c. 2 mm. long, stramineous, smooth, definitely enlarged above the middle, the enlarged portion often with a few reddish-brown cells. Calyx-lobes 6, biseriate, subequal, bent and reflexed or flaring from above the middle at anthesis, oblong-obovate, c. 0.75 — 0.9 mm. long, 0.45 — 0.6 mm. broad, rounded at the tip, entire, the midrib unbranched, the midrib area somewhat thickened and fleshy, the margins thin, scarious, subhyaline. Disk-segments 6, erect and substipitate, quadrate, c. 0.2 mm. in diameter, crenulate, pitted. Stamens 3, free except at

the very base (rarely 2 of them united), the filaments terete, erect, 0.4 — 0.5 mm. long; anthers sharply deflexed at the connectives, strongly flattened dorsiventrally, c. 0.2 mm. long, 0.3 mm. broad; anther-sacs strongly divergent, convergent at the apex but the slits not confluent; pollen grains tricolporate, c. 18 μ in diameter, angular-aperturate, the colpi narrowly bordered, not quite confluent at the poles.

Female flower: pedicel c. 10 mm. long, somewhat thickened distally. Calyx-lobes 6, subequal, oblong, c. 0.6 — 0.8 mm. long, 0.4 — 0.5 mm. broad, obtuse or acute, entire, somewhat spreading but not flaring as in the male, rather thicker and fleshier than the male, the scarious margin not so pronounced. Disk 3-angled, as of 6 segments fused in pairs, flat, thin, entire, not pitted. Ovary depressed-globose, sessile, smooth, trigonous, 6-sulcate; styles free, horizontally appressed to the ovary, 0.35 — 0.4 mm. long, bifid or ⅓-parted, the branches divergent or divaricate, the blunt tips spreading or slightly recurved.

Mature fruit and seeds not examined (ex Alain, a capsule 3 — 4 mm. in diameter).

Collected in flower in June and July.



Map III. Distribution of the American species of subg. *Cicca*.

TYPE: Cuba, Oriente, Cuchillas de Baracoa, a slender tree about 40 ft. high, flowers whitish, June 21, *Wright 1940* (GOET, holotype; G, GH, MO, isotypes; data ex GH).

DISTRIBUTION: endemic to the mountains of the Sagua-Baracoa range, Oriente Province, Cuba (Map III).

CUBA. ORIENTE: Sierra de Nipe, prope Rio Piedra, 4 Oct. 1919, *Ekman 9825* (S, HOLOTYPE of *P. punctulatus*); Moa region, Mina Cromita, Cayoguan, west of Punta Gorda, 24 July 1944, *Clemente & Alain 4079* (MICH); pineland barrens, Charrascos de Pena Prieta, Toa, alt. 600 m., 30 July 1953, *Alain 3484* (GH); same locality, 30 Dec. 1953, *Alain 3662* (GH); Baracoa, in the valley of the Rio Macaguanigua, 19 Jan. 1915, *Ekman 4323* (S, ISOTYPE of *P. brevistipulus*); Cuchillas de Baracoa, *Wright 1940* (G, GH, GOET, MO).

This extremely interesting species, although a phylogenetic relict and apparently rather rare, is not geographically narrowly confined, since its known range in the Sagua-Baracoa massif of Oriente Province is about 100 miles east to west. Its ecological requirements are not well known, the habit of pineland barrens as recorded by Alain being our only sure information. Judging from the data of Alain and others, however, it is evident that *P. pseudocicca* definitely does not occupy swamp woods or sublittoral forest habitats as do its relatives *P. acidus* and *P. elsiae*.

It is especially unfortunate that no mature fruits have been available for examination, since fruit structure is particularly significant in assessing relationships in subg. *Cicca*. The statement by Alain (Flora de Cuba 3: 53. 1953) that the fruit is a "capsula de 3 — 4 mm." may well be correct, for the ovary wall in *P. pseudocicca* at anthesis does not appear to be as thick as it is in *P. acidus;* however, the dehiscence of the fruit of *P. pseudocicca* may still not be typical for the genus. The lack of available fruits for examination is perhaps related to some peculiarity in the flowering habits of the species. Of the seven collections examined, five were completely sterile, and one of these, *Alain 3484*, was made only six days later in the year than the copiously fertile collection *Clemente & Alain 4079*.

The two species proposed by Urban, *P. brevistipulus* and *P. punctulatus*, were both founded on sterile Ekman collections. Urban compared the former to *P. nutans*, a completely different plant, and apparently was unaware that Grisebach had proposed the name *P. pseudocicca* for the same plant. Alain (loc. cit.) has already reduced *P. brevistipulus* to synonymy, and I feel certain that *P. punctulatus* merits the same treatment Urban merely compared its habit to that of *P. discolor* and *P. nutans* and added "sine dubio longe diversus." His comment was correct as far as it went, for the plant in question is indeed quite different from those two species. But Urban failed to realize that the type specimen of his *P. punctulatus* merely represents a large-leaved form of *P. pseudocicca*. The pale, slender branchlets c. 1 mm. thick, which indicate that the Ekman specimen belongs to *P. pseudocicca*, incidentally serve to distinguish this

species from another vegetatively similar Oriente species, *P. leonis*, which is often found in the sterile condition. In *P. leonis* the branchlets are mostly 1.5 — 2 mm. thick and are definitely angled.

Sect. 5. **Cicca** (L.) Muell. Arg. Linnaea **32**: 50. 1863; emend.

Cicca L. Mant. 124. 1767.
Tricarium Lour. Fl. Cochin. 557. 1790.
Staurothylax Griff. Notul. **4**: 476. 1854.
Phyllanthus sect. *Cicca* subsect. *Eucicca* Muell. Arg. loc. cit.; DC. Prodr. **15**(2): 413. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Cheramela* O. Ktze. Lex. Gen. Phaner. 434. 1904.

Trees with phyllanthoid branching, the flowers more or less cauliflorous. Monoecious or rarely dioecious. Male flower: calyx-lobes 4; disk of 4 segments; stamens mostly 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate, the colpi meeting at the poles. Female flower: calyx-lobes 4; disk lobed or separated into 4 segments; staminodes often present; carpels 3 or 4; styles free except at base, deeply bifid, spreading. Fruit drupaceous, endocarp bony; seeds 1 or less commonly 2 per fertile locule.

Type species: *Phyllanthus acidus* (L.) Skeels

The single species which comprises this monotypic section is so closely related to the representatives of sect. *Aporosella* that — despite the strong morphological discontinuity — it could almost as logically be associated with them in a single section. The production of staminodes in the female flower and the truly drupaceous nature of the fruit are the strongest distinguishing characters of sect. *Cicca*.

Robinson (Phil. Jour. Sci. Bot. **4**: 87. 1909; **6**: 323. 1911) has advocated generic status for *Cicca*, largely on the basis of the fruit, and has been followed by Merrill and other workers. There is of course no doubt that *Cicca* is a distinctive group, so that the question of its generic vs. infrageneric rank is to some extent a matter of judgment. In my opinion its close alliance with sects. *Ciccopsis* and *Aporosella* makes the inclusion of *Cicca* within *Phyllanthus* the most logical treatment.

It should be noted that the circumscription of sect. *Cicca* is here drastically altered from Mueller's concept so as to include only his subsect. *Eucicca* and to exclude his subsects. *Margaritaria*, *Prosorus*, and *Ciccoides*. Mueller's erroneous description of the fruit of *P. acidus* as capsular suggests that he had seen no good fruiting specimens and was extrapolating from the more or less dehiscent fruit of the other subsections. These latter, however, differ from *P. acidus* not only in their fruits but also in their non-phyllanthoid branching, annular floral disk, and fleshy seed-coat; indeed they scarcely have more in common with *P. acidus* than superficially rather similar tetramerous flowers. The species in these three subsections

should all be removed from *Phyllanthus* and placed together in the genus *Margaritaria*.

The following West Indian species which have been included in *Phyllanthus* sect. *Cicca* are therefore to be transferred from the genus:

1. *Phyllanthus nobilis* (L.f.) Muell. Arg. = *Margaritaria nobilis* L. f.

2. *Phyllanthus virens* (Griseb.) Muell. Arg. = **Margaritaria tetracocca** (Baill.) comb. nov. (*Wurtzia tetracocca* Baill. Adansonia **1**: 187. 1860–61).

3. *Phyllanthus scandens* (Wr. ex Griseb.) Muell. Arg. = **Margaritaria scandens** Wr. ex Griseb.) comb. nov. (*Cicca scandens* Wr. ex Griseb. Goett. Nachr. **1865**: 165–166. 1865).

4. *Phyllanthus hotteanus* Urb. & Ekm. (Ark. Bot. [Stockholm] **22A** [8]: 61. 1929) = **Margaritaria hotteana** (Urb. & Ekm.) comb. nov.

7. **Phyllanthus acidus** (L.) Skeels, U.S.D.A. Bur. Pl. Ind. Bull. **148**: 17. 1909. (PLATE XV, *figs. D–F*).

Neli-pouli Rheede, Hort. Malabar. **3**: 57, *pls. 47, 48*. 1682.
Malus indica, fructu parvo rotundo acido striato Burm. Thes. Zeyl. 148. 1737.
Averrhoa ramis nudis fructificantibus, pomis subrotundis L. Fl. Zeyl. 80. 1747.
Cheramela Rumph. Herb. Amb. **7**: 34, *pl. 17, fig. 2*. 1750.
Averrhoa acida L. Sp. Pl. 428. 1753.
Cicca disticha L. Mant. **1**: 124. 1767.
Cicca nodiflora Lam. Encycl. **2**: 1. 1786.
Cicca racemosa Lour. Fl. Cochin. 556. 1790.
Phyllanthus longifolius Jacq. Hort. Schoenbr. **2**: 36, *pl. 194*. 1797.
Cicca acidissima Blanco, Fl. Filip. ed. 1, 700. 1837.
Phyllanthus cicca Muell. Arg. Linnaea **32**: 50. 1863.
Phyllanthus cicca β bracteosus Muell. Arg. ibid.
Phyllanthus distichus (L.) Muell. Arg. in DC. Prodr. **15**(2): 413. 1866.
Phyllanthus distichus f. *nodiflorus* (Lam.) Muell. Arg. op. cit. 414.
Phyllanthus acidissimus (Blanco) Muell. Arg. op. cit. 417.
Diasperus distichus (L.) O. Ktze. Rev. Gen. **2**: 599. 1891.
Cicca acida (L.) Merr. Interpr. Rumph. Herb. 17. 1917.

A small or medium-sized glabrous tree up to 10 m. high, with rough grey bark; older branches subterete, up to c. 1.5 cm. thick, greyish brown, with rather prominent lenticels; terminal branches of current year dark brown, smooth, remaining spur-like or elongating up to c. 8 cm., 3 — 5 mm. thick, producing usually seven or eight leafy branchlets; inflorescences mostly borne on lateral spur-shoots (less than 1 cm. long) on older wood. Cataphylls blackish brown, rather firm but breaking away and not persisting, the stipules triangular-ovate, c. 1.5 mm. long, with entire to fimbriate margins; blade similar but narrower, acuminate, up to 2 mm. long. Deciduous branchlets ascending, (20–) 25 — 52 cm. long, c. 1.5 — 3 mm. thick, pale brown, terete (somewhat flattened or subangled toward apex), smooth, with 25 — 40 leaves; first internode 1 — 5 cm. long, median internodes c. 0.5 — 1 cm. long. Leaves: stipules appressed, the bases more

or less persistent, triangular-acuminate, c. 0.8 — 1.2 mm. long and (0.3–) 0.5 — 0.8 mm. broad (the proximal ones somewhat larger), not auriculate, dark brown, scarious, entire or denticulate-fimbriate. Petiole 2.5 — 4 mm. long, yellowish brown, more or less rugose, with two blunt ridges and a low median ridge on the adaxial side. Leaf blade chartaceous, broadly ovate to ovate-lanceolate, (4–) 5 — 9 cm. long, (2–) 2.5 — 4.5 cm. broad, acute (sometimes abruptly so) at the tip, obtuse or rounded at the base; above olivaceous, sublucid, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary branches evident to conspicuous; beneath pale greyish brown, the midrib prominently raised, the laterals (c. 5 — 7 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins undifferentiated, plane.

Monoecious (in West Indian material); flowers borne in dense pulviniform cymules at the nodes of "naked" branchlets on older wood, and usually also on the proximal branchlets of the current year's growth (at the tip of the branch). Cymules of cauline inflorescence axes (which are merely modified deciduous branchlets) bisexual, each with 1 — 9 female flowers accompanied by c. 25 — 40 males. First branchlets of the current year's growth often bearing bisexual cymules with 1 — 2 female flowers and a dozen (or less) males; succeeding ones with male cymules; distalmost branchlets quite sterile (sometimes no branchlets with bisexual cymules, or occasionally all branchlets sterile). Bracts of cymules blackish brown with reddish brown scarious fimbriate margins, less than 1 mm. long.

Male flower: pedicel slender, c. 1.5 — 3 mm. long. Calyx-lobes 4, subequal (the inner pair rather broader), elliptic to suborbicular, 1.1 — 1.4 (–1.5) mm. long, 0.8 — 1.3 (–1.4) mm. broad, rounded or obtuse at the tip, entire, the midrib unbranched. Disk-segments 4, more or less orbicular, c. 0.2 — 0.3 mm. across, not massive, entire. Stamens 4 (rarely 3), filaments free (at most slightly coherent at base), slender (c. 0.1 mm. thick), erect, 0.4 — 0.5 (–0.6) mm. long; anthers more or less deflexed at the connectives, emarginate or occasionally minutely apiculate, broadly elliptic to suborbicular, c. 0.25 — 0.3 mm. long, 0.3 — 0.35 mm. broad; anther-sacs parallel, dehiscing longitudinally, the slits not confluent; pollen grains 16 — 19 μ in diameter, tricolporate, not angular-aperturate, the colpi conspicuously bordered, confluent at the poles.

Female flower: pedicel straight, terete and rather stout (in fresh material; often becoming wrinkled or sharply ridged on drying), increasing in length from c. 1.2 — 1.5 mm. at anthesis up to c. 2.3 — 5 (–6) mm. in fruit, c. 0.3 — 0.5 mm. thick. Calyx-lobes 4, at first erect, later spreading, subequal, triangular-ovate or elliptic, (1–) 1.2 — 1.4 mm. long, (0.9–) 1 — 1.25 mm. broad, obtuse or rounded at the tip, thickened at the base, entire, the midrib unbranched. Disk c. 1 — 1.2 mm. across, mostly deeply lobed or separated into 4 quadrate or reniform segments, these c. 0.2 — 0.3 mm. across. Ovary at first more or less pyriform, c. 0.8 — 1.1 mm. high, 0.8 — 1.2 mm. in diameter, smooth, brownish, shallowly 3- or 4-lobed, usually definitely stipitate, the broad gynophore c. 0.2 — 0.25 mm. high;

styles very shortly connate into a column 0.2 — 0.25 mm. high, recurving, deeply bifid to the column, the slender tapering branches c. 0.8 — 1 mm. long. Staminodia 0, 1, or 2 (rarely to 4, ex Mueller) per flower, resembling the stamens but filaments much shorter.

Fruit drupaceous, oblate, of 3 or less commonly 4 carpels shallowly 6- or 8-lobed, the flesh (exocarp) firm, greenish yellow to creamy white, acid in taste, quite variable in size: when fresh, c. 1 — 1.5 cm. high, (1.2–) 1.5 — 2 (–2.5) cm. in diameter. Endocarp very hard and bony, the carpels firmly united and never separating on drying of the fruit, subglobose or oblate, deeply but obtusely ridged, c. (4.8–) 5 — 7 (–9) mm. high and 6 — 9 (–16.5) mm. in diameter. All carpels of a fruit rarely fertile, usually only 1 or 2 (–3) cells each developing 1 or less commonly 2 seeds. Seeds (when single) adaxially concave, c. 3.3 — 3.5 mm. long, 2.5 — 3 mm. broad; seed-coat thin (except around the hilum), brittle, light brown, smooth; hilum broad, circular, on the adaxial face.

Flowering (in the West Indies) mostly January through July; most flowering collections made January through March; sometimes flowering in the leafless condition, according to collectors.

TYPE: Linnaean Herbarium, sheet 592–3 (LINN). This specimen is here designated as the holotype, although ordinarily species first described by Linnaeus in the "Flora Zeylanica" would be based on specimens in the Hermann Herbarium (BM). As pointed out, however, by Trimen (Handb. Fl. Ceylon **4**: 26. 1898), there is no specimen of the plant in Hermann's herbarium, and the drawing cannot be identified with certainty. Rheede's figures are good (except that the leaves are shown as opposite!), and following the strictest priority one could make one of his two plates the type; but in view of the doubt connected with Linnaeus's original treatment, it seems preferable to typify the basionym *Averrhoa acida* by a particular specimen.

DISTRIBUTION: native probably to South America (MAP III); cultivated on all of the larger islands of the West Indies. Only representative specimens are cited.

BAHAMAS: Andros, Fresh Creek, *J. I. & A. R. Northrop 653* (F). CUBA: Las Villas, La Sierra, *Jack 7851* (A, S, US). JAMAICA: *R. C. Alexander* (GOET). PUERTO RICO: Isabon, *Sintenis 6487* (F, G). ST. CROIX: Bassin, *A. E. Ricksecker 268* (F, US). ST. THOMAS: Canaan, *Eggers 372* (G, M). ANTIGUA: *Wullschlaegel 496* (GOET). GUADELOUPE: Basse-Terre, *Duss 2929* (US). MARTINIQUE: *Duss 955* (US). ST. VINCENT: *Caley* (G, W). ISLA DE PROVIDENCIA: *Proctor 3462* (US).

Carl Linné the younger was the first to observe that *Averrhoa acida* and *Cicca disticha* were synonymous (Suppl. Pl. 416. 1781); and he also questioned the distinctiveness of *Cicca* as a genus distinct from *Phyllanthus*. The rather variable inflorescence in this species, together with the confusion introduced by Linnaeus when he redescribed it (twenty years after the "Flora Zeylanica") as *Cicca disticha*, has resulted in a rather

complicated synonymy for the plant. Lamarck's *Cicca nodiflora* was based on a specimen in which the flowers were borne on leafy branchlets rather than on naked axes on older wood; but since both conditions may normally occur on the same plant, his name does not merit retention for a taxon of any rank. Jacquin's magnificent folded colored plate in the "Hortus Schoenbrunnensis" is the best illustration yet published of this species, and clearly shows both the hermaphrodite and unisexual flower forms.

The female flowers of *P. acidus* are unique in the presence of staminodes which at times apparently act as functional stamens. The number of staminodes per flower, however, is variable even in the same inflorescence and fluctuates on the same plant from 0 to 4. No flowering herbarium specimens were seen in which there was not at least one staminode in some of the flowers. Consequently, this feature could be used in support of the claim of *Cicca* to generic status; but the evidently close relationship of the present species to the two following more than outweighs the staminodial character, which after all appears to be a sort of "teratological" reversion and not a primitive character.

The number of fertile sporophylls is variable in both the male and female flowers of *P. acidus*. However, whereas there are regularly 4-carpelled flowers mixed among the predominantly 3-carpelled ones, fluctuations in the number of stamens are less common. Some trees appear to produce regularly male flowers with four stamens, while in others (represented by the herbarium specimens *Karsten s.n.* from Merida, Venezuela (W), and *Schwanecke 12* from Puerto Rico (W)), all flowers have only two or three stamens. In the *Schwanecke* collection, there are furthermore many flowers in which a pistillode-like structure occurs. However, it appears that this "pistillode" is actually a modified stamen, for in *P. acidus* it has not been observed in normal flowers with four stamens. It might be thought that these floral irregularities in *P. acidus* are related to its cultivated state; but if one may judge from the numerical fluctuations of the floral parts of *P. elsiae*, it seems more likely that there is simply an inherent tendency toward meristic variation in the flowers of *P. acidus*.

Phylogenetically, *P. acidus* is of great interest in that it forms a connecting link between sect. *Ciccopsis* and sect. *Aporosella*. Its androecium of stamens with elongated filaments and reflexed anthers, and its well-developed floral disk, agree with sect. *Ciccopsis;* but its massive ovary developing into an indehiscent fruit, its cauliflorous inflorescence, and its leaf form are more like sect. *Aporosella*. Sect. *Cicca* further agrees with sect. *Aporosella* in its tendency toward dioeciousness; although all West Indian specimens examined are monoecious, those from the Philippines are dioecious, as pointed out by Robinson (Phil. Jour. Sci. Bot. 4: 87. 1909). On the other hand, its pollen grains appear to be somewhat less specialized than those of either *Ciccopsis* or *Aporosella*. If we conceive of the four American species of subg. *Cicca* as relict populations surviving from an anciently widespread ancestor, these cross-relationships and differential evolutions of organs can be mostly clearly and easily explained.

Heretofore, the relationships between *P. acidus* and the other American representatives of subg. *Cicca* have not been recognized, partly because of taxonomic confusion but perhaps mostly because of the prevalent misconception of the indigenous range of *P. acidus*. In common with many widely cultivated tropical plants, *P. acidus* has been regarded as of rather uncertain nativity. Nevertheless, all authors have credited the species to the Old World, and indeed most commonly to Madagascar and the Malay Islands. Trimen (Handb. Fl. Ceylon **4**: 26. 1898), for instance, observes that it is "much grown in native gardens for its acid fruit . . . and no doubt an ancient cultivation." It is recorded by Merrill (Enum. Phil. Fl. Pl. **2**: 397. 1923) as "of prehistoric introduction from Malaya." Numerous other authors could be cited in support of the "Malayan" origin of the plant, but on the other hand, there are some significant disclaimers. Thus Ridley (Fl. Malay Pen. **3**: 216. 1924) cites it only from gardens, and Burkill (Dict. Econ. Prod. Malay Pen. **1**: 537. 1935) classifies it as of "uncertain origin." J. J. Smith (Add. Fl. Arb. Jav. **12**: 82–83. 1910), a usually careful observer, notes that the species, to the best of his knowledge, has never been encountered wild in Java, although it is much cultivated there. Leandri (Not. Syst. **7**: 186. 1939) found no specimens of the species (even of cultivated trees) from Madagascar. The final impression given by a perusal of the literature is thus that of a "probably Malayan" plant which has never been discovered wild there!

In view of this nearly universal ascription of the homeland of *P. acidus* to the Indonesian region, it was a distinct surprise to find in the course of the present study that the closest congeners of the species are the two representatives of the New World sect. *Aporosella*, while on the other hand it has no close relatives in the Old World. In fact, specimens of *P. elsiae* have so often been misidentified as *P. acidus* that it is quite impossible to determine from published reports whether or not *P. acidus* is growing wild at a specific locality. Thus far attempts to discover the native habitat of *P. acidus* have been largely unsuccessful. The collections of Martius from Minas Geraes, cited by Mueller (Fl. Brasil. **11**[2]: 68. 1873), have unfortunately not been examined; but another collection from the same state (*Wawra & Maly* [W]) appears definitely to represent a cultivated plant, as do two collections made by Karsten at Merida, Venezuela, and Bucaramanga, Colombia (both at W). Only one herbarium specimen has been examined which would appear to represent *P. acidus* in its native habitat; it was collected by Poeppig in 1832 on the island of Colares in the Pará River delta, northeastern Brazil (W). Poeppig's notation that the habitat of the plant was in littoral woods ("sylvis littoreis") suggests very strongly that he was dealing with the native plant; for one would expect that *P. acidus* might have ecological requirements similar to those of *P. elsiae*.

A search through the floristic publications of Huber and Ducke on the Amazon delta region has failed to turn up any record of *P. acidus*, under its accepted or any synonymous name. This, however, would not appear to cast any doubt on the authenticity of the Poeppig collection. The coastal Amazonian region contains so many large stretches which because

of the uninviting and inaccessible nature of the terrain are little-known botanically, that the existence of *P. acidus* in considerable abundance there is by no means excluded. If it inhabits the infra-mangrove forest zone, which is relatively narrow, it may have gone undetected, just as *P. elsiae* was until the studies of Lindeman in Surinam.

It is at the very least a remarkable and interesting coincidence that there is a similar uncertainty as to the origin of the oxalidaceous mimic of *P. acidus*, *Averrhoa bilimbi* L. The superficial resemblance of the two species is so arresting that it is not surprising that Linnaeus was misled into classifying both of them as species of *Averrhoa*. The geographical problem with regard to *Averrhoa bilimbi* is made even more puzzling by the fact that there is an equal uncertainty regarding the origin of the only other species in the genus, *A. carambola*. All three of these similar plants, which Burman grouped together as species of "Malus indica" are cultivated at present in tropical gardens throughout much of America and Asia; but the two species of *Averrhoa* show a much greater tendency to become naturalized. Knuth (Pflanzenf. ed. 2, **19a**: 39. 1931) has in fact ascribed the origin of the genus to *Averrhoa* to Malaysia on the basis of the report by Koorders (Exkursionsfl. Java 2: 413. 1912) that both species are found wild in Java.

Many authors have remarked that the species of *Averrhoa* are "obviously of ancient cultivation" in the Indian and Malaysian regions. However, in view of our sure knowledge of the rapid diffusion of corn throughout the Old World (cf. Mangelsdorf & Oliver, Bot. Mus. Leafl. Harvard Univ. 14: 263–291. 1951), the possibility of a post-Columbian introduction from the New World must be admitted for *Averrhoa* as well as for *P. acidus*. Trimen (Handb. Fl. Ceyl. 1: 200. 1893) has already suggested that the two averrhoas were originally introduced into Ceylon from the New World by the Portuguese, and Merrill (Chron. Bot. **14**: 301. 1954) states positively that this was the case, though without adducing any specific evidence. The investigation of *Averrhoa* from the phytogeographic point of view is of especial interest since it appears to be the only genus of more than one species which is unknown in the indigenous state.

When all the evidence is considered, it appears that *P. acidus* certainly, and both species of *Averrhoa* probably, are indigenous to the New World and have been introduced into the Old World in post-Columbian times. Although the exact natural range of *P. acidus* is still unknown, it definitely is native to the Pará River delta, and will probably be discovered in a number of localities in the Amazon delta region. By analogy with the documented evidence for *P. acidus*, it appears most likely that both species of *Averrhoa* are also originally American plants which have had a similar history. The great superficial resemblance between these three species may not be entirely coincidence, for it is possible that all three are members of the sub-littoral forests of the South American coastline; and their similarity in life form may have a selective basis. Probably, as suggested by Merrill and Trimen, these plants were first encountered by the Portuguese on the Brazilian coast and from there carried to India and

other parts of the Old World. The fascinating problems in ethnobotany posed by such species as *P. acidus* cannot be resolved with certainty until a more thorough knowledge of the coastal flora of northeastern Brazil can be correlated with an analysis of the earliest Portuguese explorations there. When this is accomplished, a definitive evaluation can be made of the hypotheses presented here.

Sect. 6. **Aporosella** (Chodat) stat. nov.

Aporosella Chodat, Bull. Herb. Boiss. 2 ser. 5: 488–489. 1905.

Trees with completely cauliflorous inflorescences, flowering with the appearance of the leaves. Dioecious; flowers in aphyllous thyrsi (the leaves reduced to bracts). Male flower: calyx-lobes usually 4; disk absent; stamens usually 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate. Female flower: calyx-lobes 4; disk absent; staminodes absent; carpels 2 or 3; styles connate at the base, bifid or lacerate. Fruit indehiscent and woody, the endocarp bony, with 2 or 3 cells; fertile locules 1 or 2 per fruit, seeds solitary.

TYPE SPECIES: *Phyllanthus chacoensis* Morong [*Aporosella hassleriana* Chodat].

This small section of two American species is so divergent from the great majority of the species of *Phyllanthus* that on the basis of morphological characters alone it could be maintained as a distinct genus. The combination of arboreal habit, dioecious completely cauliflorous inflorescence, woody indehiscent fruit, and absence of a floral disk is unique, and indeed defines the group much more sharply from the typical species of *Phyllanthus* than do the characters which distinguish such genera as *Glochidion*, *Sauropus*, and *Breynia*. However, there can be no doubt that the two species of *Aporosella* are closely related to *P. acidus*, and through that species, perhaps via *P. pseudocicca*, to more "typical" species of *Phyllanthus* in subgenus *Kirganelia*. It would thus be manifestly contrary to natural relationship to recognize *Aporosella* as a distinct genus and at the same time leave sects. *Cicca* and *Ciccopsis* within *Phyllanthus*. A segregate genus comprising sects. *Ciccopsis*, *Cicca*, and *Aporosella* would be more satisfactory except that it would be nearly impossible to distinguish it from *Phyllanthus*. Consequently, it does not appear practicable at the present time to recognize any part or all of subg. *Cicca* as an independent genus.

Pax and Hoffmann (Pflanzenr. IV. 147. XV: 105–107. 1922) seriously erred in placing *Aporosella* in the subtribe Antidesminae between *Aporosa* and *Antidesma*. The resemblance between these three genera is confined to a superficial similarity in inflorescence and fruit; but the phyllanthoid branching of *Aporosella* clearly precludes its belonging to the Antidesminae. The original ascription of the type species to *Phyllanthus* by Morong (Ann. N. Y. Acad. Sci. 7: 218. 1892) after all comes closest to the mark.

8. **Phyllanthus elsiae** Urb. Repert. Sp. Nov. 15: 405–406. 1919. (PLATE XV, *figs. G–I*).

Glabrous small or medium-sized tree c. 7 — 15 m. high with a dense crown, the habit similar to that of *P. acidus;* older branches terete, c. 0.5 — 1.5 cm. broad, sometimes with conspicuous lenticels; branches of current year with up to 10 leafy branchlets. Cataphylls blackish brown, indurate, more or less deciduous; stipules triangular-ovate, c. 1.5 mm. long, with fimbriate margins; blade similar but narrower. Deciduous branchlets ascending, (10–) 15 — 30 cm. long, c. 1.3 — 1.8 mm. thick, pale to dark brown, obscurely angled or terete, smooth, with c. 10 — 20 leaves; first internode (0.3–) 1 — 2.5 (–4) cm. long, median internodes c. 1 — 1.5 cm. long. Leaves: stipules appressed, triangular-lanceolate, c. 0.8 — 1.2 mm. long, 0.5 — 0.7 mm. broad, acute, blackish-brown, scarious, subentire, not auriculate at the base. Petiole 2.5 — 3.5 mm. long, subterete, often corrugated, the edges of the blade decurrent on the adaxial face as two straight rather inconspicuous flanges. Leaf-blade chartaceous (sometimes stiffly so) mostly broadly elliptic to suborbicular and rather abruptly contracted to a short acumen, mostly 3 — 5 (–7) cm. long, 2 — 4 (–5) cm. broad, obtuse or rounded at the base; above olivaceous to plumbeous, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary veinlets obscure to subprominent; beneath greenish or greyish to reddish brown, the midrib prominently raised, the laterals (usually 4 or 5 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins plane or often more or less undulate or crisp.

Dioecious; flowers borne only on naked branchlets (thyrsi) on older wood of the stem (these clustered on spur-shoots in the axils of old leaf-scars), never on leafy branchlets of the current year's growth. Bracts indurate, blackish brown; stipules broadly triangular, umbonate, margins lacerate-fimbriate, c. 1 — 1.5 mm. long and 1.2 — 1.4 mm. broad, the blade c. 0.7 — 1.5 mm. long. Male inflorescence axes (1–) 1.5 — 7 cm. long, with 5 — 13 (–19) nodes; cymules with c. 10 — 20 flowers. Female inflorescence axes (2–) 3 — 6 (–9) cm. long, with 7 — 13 (–19) nodes; cymules with 1 — 3 (rarely 4) flowers.

Male flower: pedicel (1.2–) 1.5 — 3 (–5) mm. long. Calyx-lobes 4, subequal, obovate, 1 — 1.7 mm. long, 0.7 — 1 mm. broad, obtuse or rounded at the tip, entire to minutely fimbriate, the hyaline margins narrow to rather broad, midrib unbranched. Disk absent. Stamens 4 (rarely 3 or 5); filaments free, slender, erect, only 0.1 — 0.25 mm. long; anther-sacs parallel, dehiscing vertically, the slits not confluent; pollen grains 17–21 μ in diameter, slightly angular-aperturate, colpi very narrow and not meeting at the poles.

Female flower: pedicel terete or subangular, straight or curved, smooth, (1–) 1.5 — 2 (–3) mm. long. Calyx-lobes 4, subequal (the outer somewhat smaller), obovate or oblong, 0.8 — 1.3 mm. long, (0.4–) 0.6 — 0.8 mm. broad, rounded at the tip, subentire to minutely fimbriate, the midrib

unbranched. Disk absent. Ovary ovoid, c. 0.8 — 1.2 mm. in diameter at anthesis, rugulose, not stipitate, of 3 or rarely 2 carpels; styles connate at the base into a column c. 0.3 — 0.5 mm. high, bifid to the column, the flattened acute tapering tips spreading or ascending, 1.8 — 2.3 mm. long. Staminodia absent.

Fruit mostly oblate spheroidal, 3-celled (rarely 2-celled), (5–) 6 — 8.5 mm. high, (5.5–) 6 — 8.5 (–10.5) mm. broad, obtusely lobed, indehiscent, dry and woody, the outer layer soft and pithy, the inner hard and bony. Fertile carpels usually 1 or 2 per fruit, each with a single seed. Seeds flattened, smooth, the brittle testa pale brown or stramineous, c. 3 — 3.5 (–4) mm. long, (2–) 2.2 — 2.4 (–2.7) mm. broad; hilum conspicuous, c. 0.7 — 1 mm. across, dark reddish-brown, triangular or roundish.

Collected in flower January through March; in fruit April through December.

TYPE: Tobago, Auchenskeoch Beach, March 25, 1914, *W. E. Broadway 4789* (US 759650; LECTOTYPE). The specimen in the U. S. National Herbarium is here designated as the lectotype, as it is the only sheet seen of the type collection; the original specimen in Urban's herbarium at Berlin-Dahlem presumably was destroyed during World War II.

DISTRIBUTION: low forests along lagoons and rivers, usually near sea-level, northern South America to southern Mexico (MAP III).

TOBAGO: Auchenskeoch Beach, *Broadway 4789* (US, LECTOTYPE), *5910* (MO); Studley Park, near the sea, *Broadway 4557* (F, GH, MO, US). TRINIDAD: Erin, sea shore, *Broadway 7845* (MO, S), *9112* (A, MO); Rousillac Swamp, *Swabey* (TRIN 12558).

Because of the variability and interesting distribution of this species, the following representative specimens are cited from throughout its range.

MEXICO: NAYARIT: Mexcatitlan, nearly at sea level, shallow lagoons, growing in water, *Mexia 1005* (A, US); same locality, *Ortega 5545* (US). GUERRERO: near sea beach, Acapulco, *Palmer 595* (A, US). CHIAPAS: Paredon, Tonala, *Matuda 16274* (US).

BRITISH HONDURAS: Belize River, *Record B.H.52* (US).

EL SALVADOR: SANTA ANA: El Desagüe, Laguna de Quija, alt. 440 m., *Pittier 1902* (US). SAN MIGUEL: Laguna de Olomega, alt. c. 75 m., *Standley 20983* (GH). SONSONATE: Izalco, in park, *Standley 22234* (GH).

PANAMA: CANAL ZONE: banks of Chagres River, below Gatun, near sea-level, *Maxon 4797* (US); forest along the Rio Indio de Gatun, near sea-level, *Pittier 2776* (US).

COLOMBIA: BOLIVAR: San Martin de Loba, *Curran 409* (GH); river-marsh, Magangue, *Pennell 3954* (US). SANTANDER: Puerto Wilches, *Daniel 1178* (US).

VENEZUELA: DELTA: Rio Manimo, Buelta Triste, *Bond, Gillin, & Brown 158* (GH, US), *163* (GH).

BRITISH GUIANA: Botanic Gardens, Georgetown, *Archer 2576* (US).

SURINAM: swamp, Nickerie, Nanni-creek, near Kaaimancreek, common, *Geyskes 154* (A).

The broad distribution of *P. elsiae*, which is probably locally common in numbers of mainland littoral areas along the Caribbean, has not been recognized heretofore because of the confusion between it and *P. acidus*. Since the original publication of the species by Urban, all of the collections cited above with the exception of that of Swabey have either been mistaken for *P. acidus* or left unnamed. Lanjouw and Lindeman, however, have independently come to the conclusion that the tree of the Surinam swamps discussed by Lindeman (Veg. Coastal Reg. Suriname, Table II. 1953) under the name *P. acidus* actually represents a different species (personal communication).

The habitat of *P. elsiae*, as reported by Lindeman, is the swamp woods or moist forest which often occurs near the coastline directly behind the mangrove belt, and only a few feet above sea-level. Only the collection made in El Salvador by Pittier records the species at an elevation of greater than 100 meters. It is probable that further collecting will show the range of *P. elsiae* to be almost continuous along the coast from Surinam to British Honduras and, on the Pacific side, from Panama to Mexico. As far as can be determined, however, the species does not occur along the Pacific Coast of South America.

The resemblance between *P. acidus* and *P. elsiae* is so close that the past confusion is quite understandable. Both plants are cauliflorous trees with tetramerous flowers and similar indehiscent fruits. However, the differences between the two species are so important that they seem best assigned to separate sections. In contrast to the West Indian representatives of *P. acidus*, which are monoecious, with a well-developed floral disk and drupaceous fruit, *P. elsiae* is dioecious, with no floral disk and with a woody rather than fleshy fruit. Even sterile specimens of the two species are readily separable. *P. acidus* having branchlets with 25—40 leaves and ovate leaves gradually narrowed to the tip, while *P. elsiae* has branchlets with 10—20 leaves and more rotund leaves which are usually abruptly narrowed at the tip. Furthermore, *P. elsiae* is always perfectly cauliflorous (the leafy branchlets invariably being sterile), while *P. acidus* usually has flowers produced on the leafy branchlets as well as the aphyllous thyrses.

Much more closely related than *P. acidus* is the type species of *Aporosella*, *P. chacoensis*. This plant, native to the Chaco region of Argentina and Paraguay, resembles *P. elsiae* so closely that one might almost consider the two taxa as subspecies of a single species. However, the fruits of *P. chacoensis* are always 2-celled, and although this character is not invariable in distinguishing it from *P. elsiae* (which rarely has a few 2-celled fruits in addition to the usual 3-celled ones), the styles furnish an adequate diagnostic feature. They are much broader and shorter (less than 1 mm. long) in *P. chacoensis* than in *P. elsiae*. It appears best, therefore, to consider the plants in question as two closely related but distinct species.

Sect. 7. **Emblica** (Gaertn.) Baill. Etud. Gen. Euphorb. 626. 1858.

Emblica Gaertn. Fruct. 2: 122–123, *pl. 108, fig. 2.* 1790.
Dichelactina Hance in Walp. Ann. 3: 375. 1852–53.

Trees with phyllanthoid branching; branchlets often fascicled at the nodes; leaves oblong to linear, closely distichous. Monoecious; flowers in axillary cymules at the proximal nodes of branchlets. Male flower: calyx-lobes usually 6; disk of 6 small segments, or absent; stamens normally 3, filaments united into a column; anthers sessile atop the column, dehiscing vertically; pollen grains subglobose to subprolate, 4- or 5-colporate. Female flower: pedicel very short; calyx-lobes 6; disk a lacerate cup enveloping the ovary; ovary smooth, of 3 carpels; styles shortly connate, twice bifid, distally dilated. Capsule with a fleshy exocarp, the cocci rather thick and massive, eventually separating from a well-developed columella. Seeds 2 in each locule, trigonous, somewhat unequal.

Type species: *Emblica officinalis* Gaertn. loc. cit. (= *Phyllanthus emblica* L.).

This section of a few Old World species is here given the same circumscription as that of Hooker (Fl. Br. Ind. **5**: 286, 289–290. 1887), who excluded from the section all the species listed by Mueller (DC. Prodr. **15**(2): 352–355. 1866) except those with fleshy fruits. Pax and Hoffmann (Naturl. Pflanzenf. **19c**: 64. 1931) have also accepted the section in this sense. Beille, on the other hand (Fl. Gen. L'Indo-Chine **5**: 572. 1927), has continued the usage of Mueller, without however showing any convincing distinction between sect. *Emblica* sensu Mueller and sect. *Paraphyllanthus*.

It appears to me that only by adopting the narrow circumscription can sect. *Emblica* be maintained. Hooker described three new species, and two others have more recently been proposed; but all of these appear quite similar to one another and to *P. emblica*. Possibly the populations belonging to this section should be interpreted as a single widespread, variable species native from India to Malaya and China.

The present classification of sect. *Emblica* is provisional, for it does not approach very near to any of the three other sections included in subg. *Cicca*. The arboreal habit and fleshy fruit are only superficial resemblances and do not indicate any close affinity, particularly since the fruit of *Emblica* is still fundamentally capsular, in contrast to the truly drupaceous fruits of sects. *Cicca* and *Aporosella*. Furthermore, the pollen grains of sect. *Emblica* appear to differ considerably from those of the other three sections.

In the present treatment sect. *Emblica* is retained within subg. *Cicca* primarily on grounds of convenience, for it does appear to fit here better than in any other West Indian subgenus. The natural relationships of sect. *Emblica* are doubtless with Indian species of the sect. *Paraphyllanthus* sensu Mueller, such as *P. polyphyllus*, *P. lawii*, and *P. columnaris*.

9. **Phyllanthus emblica** L. Sp. Pl. 982. 1753; Muell. Arg. in DC. Prodr. **15**(2): 352. 1866; Hook. f. Fl. Br. Ind. **5**: 289. 1887.
(PLATE XV, *figs. J–L*).

Myrobalanus emblica Bauh. Pinax 445. 1623.
Nili-camarum Rheed. Hort. Malabar. **1**: 69, *pl. 38*. 1672.
Phyllanthus foliis pinnatis floriferis, caule arboreo, fructu baccato L. Fl. Zeyl. 158. 1747.
Emblica officinalis Gaertn. Fruct. 122–123, *pl. 108*, *fig. 2*. 1790.
Emblica grandis Gaertn. op. cit. 123.
Emblica arborea Raf. Sylva Tellur. 91. 1838.
Diasperus emblica (L.) O. Ktze. Rev. Gen. **2**: 599. 1891.

A deciduous tree up to c. 15 m. high, with flaking bark; annotinous branches smooth or hirsutulous, terete or somewhat angled, greyish or brownish, 2 — 5 mm. thick, with internodes mostly 1 — 3 cm. long. Cataphylls inconspicuous, subpersistent, dark reddish brown, scarious and brittle; stipules triangular-ovate, c. 1.3 — 2 mm. long, 0.8 — 1.3 mm. broad, acuminate, margins entire or denticulate, ciliolate when young, subauriculate at the thickened base; blades basally convex and much thickened, attenuate-acuminate, c. 1.5 — 1.9 mm. long. Deciduous branchlets (5–) 10 — 25 (–30) cm. long, pale brown, furrowed, copiously hirsutulous, terete, sterile or floriferous (and then shorter), with (15–) 30 — 100 (–150) leaves, the internodes very much shorter than the imbricate leaves (i.e., mostly 1 — 3 mm. long); fertile branchlets with leaves greatly reduced in proximal floriferous portion. Leaves: stipules triangular, 0.8 — 1.5 mm. long, 0.3 — 0.5 mm. broad, apex attenuate, ciliolate, minutely denticulate, becoming dark reddish-brown and scarious. Petioles stout, 0.3 — 0.7 mm. long. Leaf blades smooth, chartaceous, linear-oblong, obtuse, slightly oblique and subcordate at the base, mostly 12 — 20 mm. long and 2 — 5 mm. broad (reduced leaves associated with flowers considerably smaller); above olivaceous, the midrib and laterals often raised and conspicuous, beneath greyish or brownish, the midrib raised, the laterals (4 — 7 on a side) straight, steeply ascending; margin firmly thickened and sometimes scarious, more or less inflexed or involute, the scarious tip of the blade more or less inflexed.

Monoecious; first few proximal nodes of floriferous branchlets barren, with leaves reduced to dark brown scarious cataphylls; succeeding nodes with green but reduced leaves subtending cymules of male flowers, followed by nodes each with a cymule of one central female flower and several lateral males, the reduced leaves of this vicinity grading into normal leaves; distal half of floriferous branchlets normally sterile, with typical leaves, less commonly the distal portion not developed.

Male flower: Pedicel glabrous, slightly thickened above, c. 1 — 2.5 mm. long (up to 4 mm. long ex Mueller). Calyx-lobes 6, oblong-obovate or spathulate, 1.2 — 2.3 mm. long, 0.5 — 1 mm. long, obtuse or rounded, convex above, entire or obscurely denticulate, membranous, yellowish white, the midrib unbranched or with a few inconspicuous branches. Disk-segments 6, clavate, crenulate, foveolate, c. 0.2 — 0.3 mm. across; or disk sometimes obsolete. Stamens 3; filaments completely united into a terete column (0.2–) 0.3 — 0.7 mm. high; anthers sessile atop the column but discrete, erect, oblong, minutely apiculate, 0.5 — 0.9 mm. long, 0.5 — 0.6

mm. broad; anther-sacs parallel, dehiscing vertically, discrete, the slits not confluent; pollen grains (ex *Broadway 5258*) subglobose, 17.5 — 19 μ in diameter, 4- or 5-colporate, the colpi short, not bordered.

Female flower subsessile, the ill-defined pedicel 0.5 mm. long or less. Calyx-lobes 6, oblong or spathulate, 1.6 — 2.5 mm. long, 0.7 — 1.3 mm. broad, obtuse or rounded at the tip, more or less obscurely denticulate, thicker than the male, the scarious margin ill-defined or obsolete, Disk urceolate, investing the ovary, up to c. 1 mm. high, 6-ribbed, the ribs alternate with the calyx-lobes and projecting as marginal fimbrillae, the rim often with smaller teeth between the projecting ribs. Ovary smooth, ovoid; styles rather fleshy, shortly connate at the base, c. 2.5 — 4 mm. long, ⅓-parted to bifid, the branches bifid, remaining terete or flattened and conspicuously dilated and petaloid, usually spreading and distally reflexed.

Capsule with a firm fleshy greenish white or yellowish white epicarp, c. 2.5 — 3 cm. in diameter when fresh, the endocarp (cocci proper) rather massive and thick-walled, c. 1 cm. in diameter, the cocci at length separating from the columella; columella trigonous, slender below the dilated apex, c. 7 — 8 mm. high. Seeds of the pair in each coccus more or less unequal; the smaller plano-convex, 3.9 — 4.3 mm. long, c. 2.5 mm. radially, c. 2 mm. tangentially; the larger asymmetrically trigonous (carinate on one side), c. 4.5 mm. long, 3.1 — 3.2 mm. radially, c. 3 mm. tangentially; seed-coat dark chestnut brown, smooth, at high magnification with close-set rounded slightly convex flecks.

TYPE: left undesignated. There appears to be no specimen of *P. emblica* in the Hermann Herbarium (BM), and indeed Linnaeus cited none in the "Flora Zeylanica." There is a sterile specimen, number 1105–11, in the Linnaean Herbarium (LINN), which is probably this species; it is marked "H U," presumably indicating that it was grown in the botanic garden at Upsala. However, in view of the taxonomic uncertainty with regards to the limits and subspecific variation of *P. emblica*, it seems unwarranted to designate either this specimen or such illustrations as those of Rheede as representing the holotype. Typification of this Linnaean species must await a thorough study of the entire sect. *Emblica*.

DISTRIBUTION: *P. emblica,* in the present inclusive (though not necessarily correct) sense ranges from India and Ceylon to Hainan, Borneo, and Java. Mueller's reports of the species from Japan and the Mascarene Islands appear to be based on cultivated specimens. In the West Indies *P. emblica* is found only in cultivation and shows no signs of becoming part of the spontaneous flora.

BERMUDA: Public Garden, St. George's, *Brown, Britton, & Wortley 1732* (GH, NY).

CUBA: PINAR DEL RIO: Pinar del Rio City, Finca del Obispo, *Ekman 18643* (S). HABANA: Habana, *Marie-Victorin 45025* (MT). LAS VILLAS: Soledad, *Jack 4246* (NY, S).

PUERTO RICO: MAYAGUEZ: Agricultural experiment station, Mayaguez, *N. L. & E. G. Britton 7441* (NY).

LESSER ANTILLES: GRENADA: Botanic station, *Broadway* (NY).
TRINIDAD: Botanic gardens, St. Ann's, *Broadway 5238* (MO, S).

This species, widely cultivated in tropical regions, is perhaps the most economically important in the genus. Because of the use of the fruits as a purgative, it was the first species of *Phyllanthus* to become familiar to Europeans; pharmacists knew it as "emblic myrobalan" in Medieval times. However, it is also of some value as a timber tree (Pearson & Brown, For. Ind. **2**: 878–881. 1932), and as a source of tannin (Burkill, Dict. Econ. Prod. Mal. **1**: 920. 1935).

The great variability of the species is apparent even from the small sample of West Indian specimens, on which the description is mainly based. Both Mueller and Hooker reported the disk as absent in the male flowers, but in two of the flowering collections from the West Indies it is well developed as in the floral illustration of Wight (Icon. Pl. Ind. Or. **5**: *pl. 1896*. 1852). The fruit of the tree in the garden at Soledad, as observed from both herbarium (*Jack 4246*) and fresh material, is at least 2.5 cm. in diameter, which is much larger than that allowed by Hooker and better matches his *Phyllanthus pomiferus* [*Cicca macrocarpa* of Kurz]. The pollen grains of *Jack 4246*, not included in the description because they seem abnormally wrinkled, are subprolate, measuring c. 21 — 23 by 19 — 21 μ, and appear all to be 5-colporate.

The West Indian specimens appear to deviate from the norm of *P. emblica* somewhat in the longer branchlets with often an unusually large number of leaves. In *Broadway 5238* many of these long sterile branchlets are associated at a node with an abbreviated floriferous branchlet in which the distal leafy portion has been suppressed; such a marked dimorphism between fertile and sterile branchlets appears, however, to be rare. The fascicled branchlets which account for part of the characteristic appearance of the branches of *P. emblica* are, on close inspection, invariably found to be grown out from several collateral buds at a node from which the branchlet of the previous year has fallen.

Despite all these deviations, however, the West Indian collections show a close agreement in the apiculate anthers, unusual hypogynous disk, branchlet structure, and leaves; it therefore appears likely that they represent only variations of a single species.

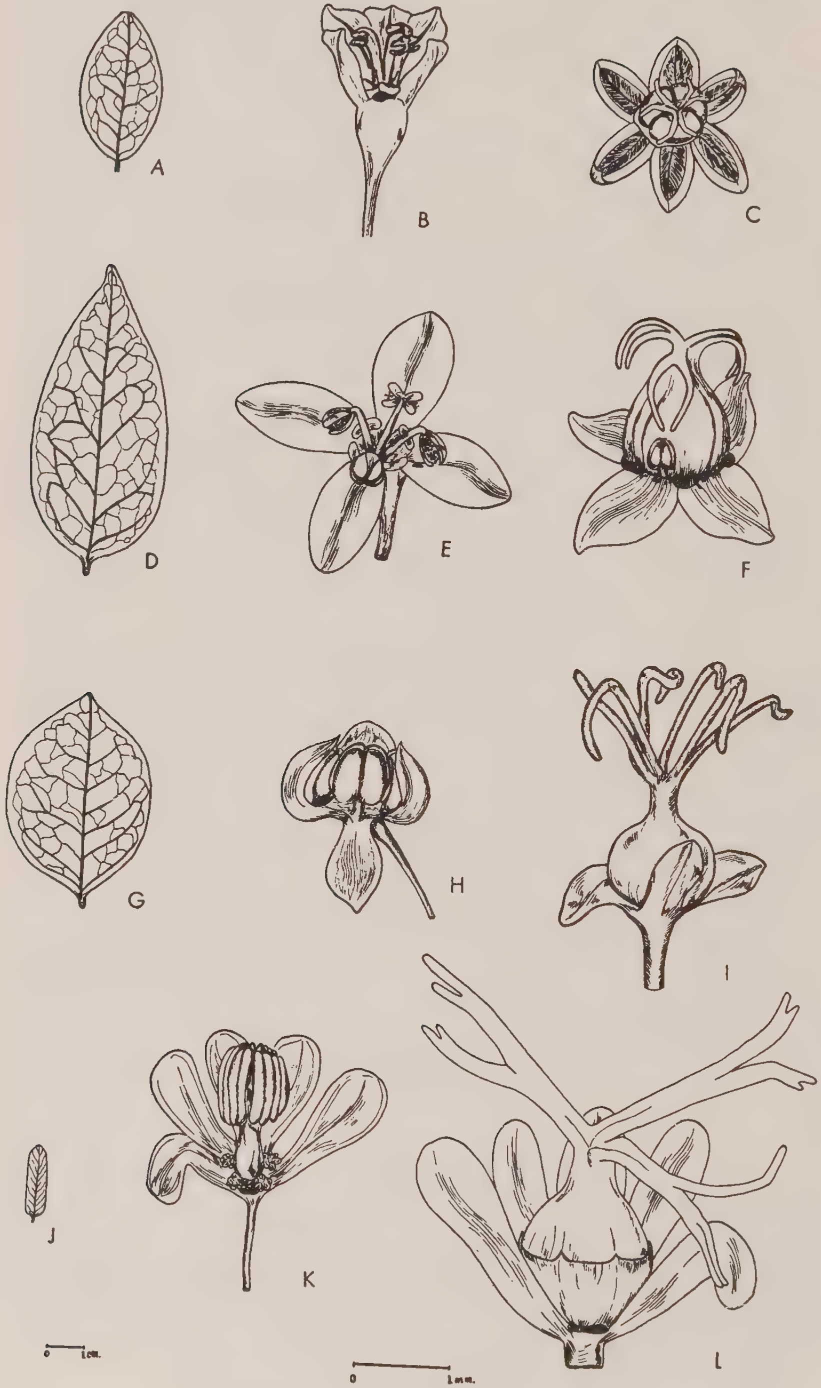
(*To be continued*)

PLATE XV

LEAVES, MALE FLOWERS, AND FEMALE FLOWERS IN SUBG. *Cicca*.[13]

FIGS. A–C. *Phyllanthus pseudocicca* Griseb. (*Clemente & Alain 4079* [MICH]). FIGS. D–F. *Phyllanthus acidus* (L.) Skeels (cult., Kingston, Jam.). FIGS. G–I. *Phyllanthus elsiae* Urb. (G, H, *Matuda 16274* [US]; I, *Palmer 595* [GH]). FIGS. J–L. *Phyllanthus emblica* L. (J, K, *Broadway 5238* [S]; L, *Tsui 118* [A]).

[13] Male and female flowers are drawn to the same scale.



Webster, West Indian Phyllanthus

STUDIES IN THE GENUS COCCOLOBA, III. THE JAMAICAN SPECIES

Richard A. Howard

In a revision of any West Indian genus of plants having wide-ranging species, the taxonomist invariably must center part of his study on the vegetation of the island of Jamaica. The specimens and the writings of the early botanists and naturalists in Jamaica, men like Hans Sloane and Patrick Browne and Olaf Swartz were accepted by Linnaeus and became the types and starting points for study of important taxa in the Caribbean vegetation. In the difficult genus *Coccoloba*, it has been necessary to spend a disproportionate amount of time on the few wide-ranging species and the great variety of names and applications given them. The lack of consistency in the successive publications of Lindau as the most recent monographer of the genus, Grisebach, Eggers, Britton and others has increased the task of assigning the proper name to each taxon. The failure of these writers to understand the normal and abnormal variations of these plants as seen in herbarium sheets has added to the difficulties of modern identification and definition.

Fawcett & Rendle, in preparing a treatment of the genus for the Flora of Jamaica, examined the Linnaean species of *Coccoloba* and published a note on these in the Journal of Botany in 1913. This was followed in 1914 with a treatment of the genus as it occurs in Jamaica and in this work eighteen species were recognized and defined in addition to one species which was recorded as "insufficiently known." Since that time only one species has been described as new to the flora of Jamaica and no species have been added to the flora by published extensions of ranges, although many erroneous herbarium identifications might have been so considered.

Fawcett & Rendle's treatment of the genus in the Flora of Jamaica is unfortunately based on an inadequate knowledge of the genus as indicated at the beginning in the generic description. The functionally unisexual flowers; the occurrence of pistillate flowers singly and the staminate flowers in multiples at the nodes of the inflorescence; the variation between adventitious and normal growth in pubescence, leaf size and leaf shape; the ability of the plants to flower in juvenile or adventitious leaf condition; the phenomenal morphological variation following injury and the frequent occurrence of hybrids, particularly those involving *Coccoloba uvifera*, are characteristics which only careful field experience could evaluate and which have not been taken into account in the generic treatment in the Flora of Jamaica.

In preparation for this paper, I have had the unusual opportunity of field work expressly for the study of *Coccoloba* populations, as well as trips which permitted attention to species of this genus. I am indebted to the American Philosophical Society for a grant from the Penrose Fund which

made possible an extended field trip in 1950 and a study of this genus from Trinidad to Cuba in the West Indies. More recently, with the aid of grants from the Institute of Jamaica and the support of both the Reynolds Jamaica Mines Company and the Kaiser Bauxite Company, I have made several field trips to Jamaica in order to study plants growing on bauxite soils, among them species of *Coccoloba*. I am grateful to the directors of these organizations for the support and cooperation offered during my visits. In the summer of 1955 while in Europe to attend the International Horticultural Congress, it was possible to visit many herbaria and gardens where the species of *Coccoloba* in the herbaria and under cultivation were studied. In addition, I have borrowed herbarium material from many botanical organizations and am appreciative of the use of material from the following herbaria cited in this paper: Arnold Arboretum (A), Berlin Botanical Garden (B), British Museum (BM), Copenhagen (C), Chicago Natural History Museum (F), University of Göttingen (Gott.), Gray Herbarium (GH), University College of the West Indies (J), Institute of Jamaica (IJ), Kew (K), Linnaean Society of London (L), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Naturhistoriska Riksmuseum, Stockholm (S), U.S. National Herbarium (US). Only the basic synonymy and most important references are given for each species. The older references for these species are published in Lindau's monograph.

Coccoloba P. Br. ex L. Syst. Nat. ed. 10, 1007, 1367. 1759. Taxon 3: 114, 156, 233. 1954, nom. conserv.

Guaiabara Miller, Gart. Dict. ed. 4, **2**: 1754.
Coccolobis P. Br. Civ. Hist. Jam. 209, *pl. 14, f. 3.* 1756.

Shrubs or trees, often with scandent branches or vines; branches terete, often geniculate, or arranged in one plane, short shoots commonly developed laterally or the terminal shoots of limited growth becoming long shoots; nodes commonly tumid; ochreae characteristically developed, membranaceous or coriaceous, deciduous or persistent, or so in part, glabrous, puberulent or pilose; leaves alternate, minute to large, membranaceous, chartaceous or coriaceous, the margin entire to undulate, flat or revolute, the primary veins straight to the margin, much branched at the apex becoming reticulate or arcuate and anastomosing or arcuate and bifurcate-anastomosing, the secondary venation obscure or coarsely to minutely reticulate, the upper leaf surface commonly pitted, rarely pubescent, the lower leaf surface glabrous to pilose, short multicellular glands present or the glands depressed in the lamina producing resinous secretions; petioles terete to stout, broadly and shallowly canaliculate above, pilose to glabrous, the base often tumid, attached at the base of the ochreae or above the base to two-thirds the length of the ochreae; plants dioecious or monoecious; inflorescence racemose or sub-spicate, spicate or paniculate, terminal on the primary or lateral branches, few-flowered and short to many-

flowered and several times the length of the leaves, the rachis glabrous, puberulent, pilose or with glandular excretions; flowers unisexual or functionally so, the staminate flowers in clusters of two to four at each node of the inflorescence, occasionally solitary, the pistillate flowers solitary; bracts subtending each node, the flowers developing in a membranaceous sheath which ruptures irregularly or regularly to become an ochreola, the ochreolae membranaceous, generally one per flower, occasionally more by abortion of flowers, rarely stalked, the flowering pedicels shorter than the ochreolae to many times as long, the flowers articulated at the apex of the pedicel; perianth campanulate at the base forming a hypanthium, the lobes 5, imbricate, the outer three slightly larger than the inner, the stamens 7 or 8 borne on the hypanthium, the filaments united at the base, the anthers introrse, the stamens in the pistillate flowers rudimentary, the pistil rudimentary in the staminate flowers, trigonous in the pistillate flowers, the styles 3, dilated at the apices, the ovary 1-celled, the ovule solitary, attached basally; perianth expanding in fruit, the lobes surrounding the achene or the hypanthium expanding surrounding the achene with the perianth lobes appressed against the apex of the achene or coronate on the achene, the achene with a hard shiny outer layer, the inner layer papery; seed with ruminated endosperm, the major lobes 3, the minor lobes and involutions numerous, the embryo centrally located, the cotyledons orbicular, flat, rarely folded, the radicle small, terete.

Type species: *Coccoloba uvifera* L.

Key to the species found in Jamaica

A. Inflorescence paniculate.
- B. Pedicels 0.5 mm. long, shorter than the ochreolae in flower, to 1.5 mm. long, slightly exceeding the ochreolae in fruit; leaves rounded to cordate at the base, deciduous, the tree often barren of leaves for short periods. .... 1. *C. plumieri.*
- BB. Pedicels 3–6 mm. long, exceeding the ochreolae in flower and in fruit; leaves broadly cuneate at the base, the tree apparently never devoid of leaves. .... 2. *C. proctori.*

AA. Inflorescence racemose, the racemes solitary or rarely with 1 or 2 smaller ones at the base.
- B. Leaves thick, generally broader than long; plants of sea coast. .... 3. *C. uvifera.*
- BB. Leaves membranaceous to thinly coriaceous, longer than broad.
  - C. Pedicels shorter or only slightly exceeding the ochreolae.
    - D. Ochreolae several, persistent, conspicuous; rachis stout; pedicels very short; leaves usually turning black on drying. .... 4. *C. swartzii.*
    - DD. Ochreolae solitary, deciduous; leaves buff or tan on drying.
      - E. Inflorescence shorter than the leaves; the blades ovate, acuminate at the apex, cordate at the base, usually exceeding 7 cm. in length; inflorescence rachis conspicuously angled; with pedicels ascending; fruit ovoid, averaging 9 mm. long and 8 mm. in diameter. .... 5. *C. troyana.*

EE. Inflorescence exceeding the leaves; blades ovate-oblong, acute at the apex, obtuse or rounded at the base, usually less than 5 cm. long; inflorescence rachis not angular, the pedicels diverging at right angles; fruit strongly 3-lobed at the base, 5 mm. long and 3 mm. diameter on the average. .... 6. *C. krugii.*

CC. Pedicels conspicuously exceeding the ochreolae in flower and fruit.

D. Leaves borne above the base of the ochreae, the base of the ochreae at leaf attachment generally conspicuously swollen.

E. Leaves appearing to be clustered on short lateral shoots, membranaceous, ovate-elliptical; inflorescence generally curved or drooping, pedicels thin. .... 7. *C. tenuifolia.*

EE. Leaves coriaceous, oblong elliptic, generally spaced on the branches which are often wand-like or scrambling; inflorescence stout, generally straight and erect; pedicels stout. .... 8. *C. longifolia.*

DD. Leaves borne at the base of the ochreae without conspicuous swelling evident.

E. Leaf blades usually oblong-elliptic, rounded at the apex, generally darkening on drying but uniform in color on both sides. .... 9. *C. diversifolia.*

EE. Leaf blades broadly elliptic to rounded-elliptic, the apex acute or acuminate; blades turning black above on drying, usually lighter below. .... 10. *C. zebra.*

1. **Coccoloba plumieri** Griseb. Fl. Brit. W.I. 162. 1859; Lindau, Engl. Bot. Jahrb. 13: 134. 1890, Symb. Antill. 1: 220, 1899; Fawcett & Rendle, Flora Jam. 3: 113. 1914.

Coccoloba polystachya Wedd. var. *jamaicensis* Fawcett & Rendle, Jour. Bot. **51**: 125. 1913, Flora Jam. **3**: 112. 1914.
Uvifera plumieri O. Ktze. Rev. Gen. **2**: 562. 1891.

Trees to 60 ft. tall, trunk diameter breast height 18 in.; bark scaly; crown dense, branches spreading; the branchlets stout, terete, lightly striate; nodes only slightly enlarged; ochreae large, 10–15 mm. long, obliquely truncate, membranaceous at the apex and deciduous, coriaceous and persistent at the base, puberulent when young, soon glabrate; petioles 3–5 cm. long, attached at the base or below the middle of the ochreae, puberulent or glabrate; leaf blades oblong-elliptic, broadly ovate or oval, membranaceous to subcoriaceous 32 × 20; 27 × 16; 20 × 13, 13 × 7 cm. glabrous; apex obtuse to bluntly acuminate; base cordate, rarely truncate; margin entire, flat or slightly undulate; midrib and primary veins evident above, prominent below, primary veins 7–9 pairs, arcuate ascending, anastomosing near the margin, ultimate venation reticulate, evident but not prominent on both surfaces; inflorescence terminal paniculate, often uniformly branched from the base, the branches 15–25 cm. long and broad, rachises angular, puberulent or glabrate; flower nodes distinct; bracts semiorbicular, minute, less than 0.5 mm. long; ochreolae membranaceous, minute, less than 0.5 mm. long; flowering pedicels minute, less

than 0.5 mm. long; fruiting pedicels to 1.5 mm. long; pistillate flowers always solitary; staminate flowers 1 to few at each node, perianth tube 1.5–2 mm. long, perianth lobes broadly ovate to suborbicular 2–3.5 mm. long and wide, functional stamens with filaments 3 mm. long at anthesis, the anthers 1 mm. long; pistillate flowers with rudimentary stamens 0.5–1 mm. long; functional pistil 2–3 mm. long, the pistil of staminate flower rudimentary 1 mm. long; fruit ovoid, rounded or subtruncate at the base, slightly narrowed at the apex to the subcoronate perianth lobes, 15–17 mm. long, 10–13 mm. thick, the lobes 2–3 mm. long; fruit perianth heavily and coarsely fibrous; achene pale brown, obtusely 3-angled, strongly apiculate at the apex.

Clarendon: Spaldings *Dignum 68* (IJ). **Manchester:** Mandeville, *Britton 3233* (NY); Moorlands Estate, 2 miles NE of Spur Tree, *Howard & Proctor 14439* (A), *Proctor 10593* (IJ). **St. Ann:** Soho, *Harris 12023* (F, MO, NY, US); Lydford Post Office, *Howard & Proctor 13398* (A, IJ), *14247* (A), *Proctor 8637* (IJ), *8687* (A). **St. Elizabeth:** Pepper, *G. S. Miller 1366* (US). **Westmoreland:** *Purdie s.n.* (K, TYPE of *C. polystachya* var. *jamaicensis;* NY, drawing). Without locality: *Alexander*, collected in 1850 (Gott. TYPE; NY, B, G), *March 1941* (B, Gott.).

COMMON NAME: Wild Grape. Collected in flower: January, July. Collected in fruit: December, January and April.

Coccoloba plumieri is the only species of the genus in Jamaica which is completely deciduous. Harris in his field notes reports plants from St. Ann to be in leafless condition in April and May. Proctor and I found plants with very young leaves just developing on plants in St. Ann in late December. As in many tropical trees, the young leaves of *C. plumieri* are limp and hanging when young and increasing in size. They become firm and coriaceous only when fully developed in size. The young leaves seen were often attractively colored red or bronze.

In the original description of *C. plumieri* Grisebach described the inflorescence of these plants as "racemes compounded at the base." His description was based on collections by Prior and March in the herbarium at Göttingen which I have seen. In both of these specimens the central axis of the inflorescence is not well developed. Lindau considered the inflorescence a panicle and placed the species in his section *Eucoccoloba* on this basis. I have now seen the specimens cited above and numerous plants in the field and agree with Lindau and Fawcett & Rendle that the inflorescence should be considered a panicle in that the central axis is dominant in most specimens but can be weak and less conspicuous than the basal branches in others. The dominance of the basal branches seems exaggerated in the fruiting condition with the weight of the mature fruit on the inflorescence diminishing the evidence of the panicle form.

Lindau's elaborate description of *C. plumieri* is confused through his failure to recognize the functionally unisexual condition of the flowers. Both staminate and pistillate flowers have been seen in the field and are represented in the collections cited. Few of the staminate flowers are

clustered and the pistillate flowers are always solitary at the nodes. Flowers of both sexes are articulated to the pedicels. The staminate flowers dehisce from the pedicels after shedding the pollen and the pedicels remain small. The pedicels of the pistillate flowers, however, increase slightly in length and thickness as the fruit develops until at maturity they are several times the length of the ochreolae. Grisebach emphasized with italics in the original description the "pedicels jointed at the base." Examination of the specimens in the Herbarium at Göttingen indicates that Grisebach had confused the scar left by the deciduous ochreolae for an articulation at the base of the fruit-bearing pedicel. While the pedicel bearing the fruit is smaller at the basal end, there is no true articulation present at that point.

Harris has suggested the common name of wild grape for this plant in the vicinity of Soho, St. Ann. I have not found a common name in legitimate use in the areas where I have collected specimens. The few fruits seen in the field were dark purple in color and astringent to taste.

A collection by Gerrit S. Miller was identified as *Coccoloba rugosa*, but should be referred to the present species. The specimen is sterile and was collected apparently from a fast-growing shoot. The single leaf available is suborbicular in shape and 32 × 32 cm. long and broad. Adventitious shoots were seen on several large trees on the Moorlands Estate and younger plants with fast-growing branches and leaders were also abundant. In all of these specimens studied in the field, the shape of the leaves on these fast-growing shoots tended to be broadly ovate to oblong-elliptical. Typical leaves from these shoots reached 40 × 20 cm. in size.

Fawcett & Rendle described a specimen collected by Purdie in 1844 in the interior of Westmoreland as *Coccoloba polystachya* var. *jamaicensis*. The specimen is from a staminate plant and can be referred without hesitation to *C. plumieri* Griseb.

2. **Coccoloba proctori**, sp. nov.

Frutex, ramulis crassis teretibus; nodis non tumescentibus; ochreis membranaceis, glabris, 10–17 mm. longis, ad basim persistentibus coriaceis, ad apicem obliquis, membranaceis; petiolis crassis, 2–3 cm. longis, glabris; lamina ovata vel elliptici-ovata, 17 × 12 vel 19 × 15 cm. longa et lata, apice obtusa, basi late cuneata vel rotundata, glabra, coriacea, nerviis primariis 4 vel 5, arcuatis inconspicue anastomosantibus; inflorescentibus terminalibus, paniculatis, ♂ ad 15 cm. longis, fructibus ad 25 cm. longis; floribus ♂ 2–4 per nodulum, floribus ♀ 1 per nodulum, rhachi glabra, bracteis 0.5 mm. longis, ochreolis membranaceis 1 mm. longis, pedicellis floriferis 3–4 mm. longis, pedicellis fructiferis 5–6 mm. longis; fructu globoso, 1 cm. diametro, lobis perianthii basi subcoronata, hypanthii 13–15 vascularibus cristis, basim versis rotundata, substipitata. Achenia pallida fulva.

Tree, branches stout terete, nodes not swollen; ochreae 10–17 mm. long, glabrous, membranaceous above and deciduous, coriaceous and persistent

below, oblique and slightly bilobed; petiole inserted at the base, petiole stout, 2–3 cm. long, glabrous, blade ovate to elliptical-ovate 17 × 12, 19 × 15 cm. long and broad, apex obtuse, base broadly cuneate to rounded, glabrous, coriaceous, primary veins 4–5 pairs, arcuate, inconspicuously anastomosing; inflorescence terminal, paniculate, staminate to 15 cm. long, fruiting to 25 cm. long, glabrate, staminate flowers in clusters of 2–4, pistillate flowers solitary, bracts less than 0.5 mm. long, ochreolae less than 1 mm. long; flowering pedicels 3–4 mm. long, glabrate, fruiting pedicels 5–6 mm. long; fruit globose, 1 cm. diameter, fruiting perianth with 13–15 vascular ridges, slightly coronate at the apex, base rounded, very slightly stalked, achene tan.

St. Elizabeth: Wooded area on limestone outcrop near Pit 101 of Kaiser Mines, south of Gutters, *Howard and Proctor 14555* (A, IJ), *15718* fruit (TYPE A), *14719* ♂ (A).

Several plants are known of this new species, but it has been found on only two limestone outcrops in the valley south of Gutters. The two largest trees were 50 and 65 feet tall and three feet in diameter at breast height. One of these has been collected in fruit twice (December and January) and the other has not been found in fertile condition. The collection *14719* was a slender tree 30 feet tall and 6 inches in diameter at breast height. Its perilous position on eroded limestone necessitated felling this tree to collect material and it was the only staminate tree seen. Numerous small trees have been located in this area and vigorous shoots of these, as well as of the larger trees, show the typical larger leaves now expected in this genus on thick shoots. The largest leaves of the adventitious shoots were on petioles of 5 cm. with blades 40 × 25 cm.

This species is named in honor of Mr. George Proctor of the Institute of Jamaica, who has been my companion on many recent field trips in Jamaica. His efforts in collecting have already resulted in making the flora of Jamaica better known.

Coccoloba proctori is similar to *C. plumieri*, differing, however, in the more strict branches of the inflorescence, the globose fruit and the leaves with cuneate bases and fewer veins.

3. **Coccoloba uvifera** L. Syst. Nat. ed. 10, 1007. 1759; Lindau, Engl. Bot. Jahrb. 13: 204. 1890, Symb. Antill. 1: 231. 1899; Fawcett & Rendle, Fl. Jam. 3: 119. 1914.

Polygonum uvifera L. Sp. Pl. 365. 1753.
Guaiabara uvifera (L) House, Am. Midl. Nat. 8: 64. 1922.

Tree of strand areas, 2–15 m. tall; branches terete, stout, papillose to pilose, the nodes not tumid; ochreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, puberulent to pilose; petioles stout, 7–10 mm. long, papillose to pilose; leaf blades orbicular to reniform, 6 × 8, 11 × 13, 13 × 18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the

midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, secondary venation minutely reticulate or obscure; apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extended around the petiole; leaves of adventitious or fast-growing shoots usually variable in size and shape, but commonly obovate; inflorescence stout, 15–13 cm. long, rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ochreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long, the fruit obpyriform, 1.2–2 cm. long, 8–10 mm. in diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, perianth rose-purple when mature, the achene black.

DISTRIBUTION: General along beaches of Florida, Bermuda, the Bahamas through the Caribbean area to South America.

Manchester: Alligator Pond, *Miller 1403* (S). **Portland:** Port Antonio, *Fredholm 3039* (US), *Proctor 11884* (IJ), *Shreve 25674* (Wisc.); Bennett Point, *Proctor 11844* (GH); Buff Bay, *Maxon 10337* (S, US). **St. Ann:** *Hunnewell & Griscom 14306* (GH); Runaway Bay, *Pierce 26* (IJ); Dunn's River, *Barkley 22J360* (IJ). **St. James:** Montego Bay, *Maxon & Killip 1639* (A, F, GH, US), *Barry s.n.* (IJ), *Davis s.n.* (Mich.). **St. Mary:** Rio Nuevo, *A. von der Porten s.n.* (IJ). **Westmoreland:** Negril Point, *M. L. Farr s.n.* (IJ). Parish uncertain: Glenwood, *Harris 5978* (F).

LOCAL NAME: Sea Grape, Seaside Grape, Beach Grape. Collected in flower in March. Collected in fruit in September.

As frequently happens with well-known and widely distributed species, *Coccoloba uvifera* has been neglected by collectors in Jamaica and is poorly represented in herbaria. The sea grape, however, is a common and often picturesque component of the strand and beach floras of Jamaica and is probably found in every coastal parish. On the north coast the sea grape has been observed only along the immediate coastline, but on the southern side of the island in the vicinity of Kingston and again on the Lititz savannah in St. Elizabeth, *C. uvifera* has been found growing several miles inland.

4. **Coccoloba swartzii** Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890, Symb. Antill. **1**: 227. 1899; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 324. 1956.

Coccoloba barbadensis, authors not Jacq.
Coccoloba diversifolia Fawcett & Rendle, Flora Jam. **3**: 115. 1914 and all recent authors not Jacq.

Coccoloba neglecta Fawcett & Rendle, Jour. Bot. **51**: 124. 1913, Flora Jam. **3**: 116. 1914.
Uvifera swartzii Ktze. Rev. Gen. **2**: 562. 1891.

Tree 8 to 20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ochreae 10–12 mm. long, the persistent coriaceous basal portion 3–5 mm. long, the upper deciduous portions membranaceous, puberulent or glabrate; petiole attached at the base of the ochreae, glabrous or puberulent becoming glabrate, 10–18 mm. long; leaf blades ovate to elliptic, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, the apex acute or rounded, the base narrowed, rounded or slightly obliquely cordate; midrib and veins inconspicuous above, prominent to inconspicuous below, the primary veins 6–7 pairs, arcuate, anastomosing, ultimate venation conspicuous reticulate; margin entire, slightly recurved; leaves of adventitious shoots with petioles 1.5–2.5 cm. long, the blades ovate to lanceolate, the apex acute to acuminate, 23 × 8.5 to 45 × 18 cm. long and broad; inflorescence terminal 10–15 cm. long, the rachis glabrous or with glandular exudates, rarely papillose, staminate flowers in clusters of 3–5 with tightly concentric membranaceous ochreolae forming a truncate or flattened cylinder after flowering; pistillate flowers solitary, ochreolae erect in flower, flattened against the rachis in fruit; bracts ovate, 1–1.5 mm. long, ochreolae membranaceous 1–1.5 mm. long, flowering pedicels shorter than the ochreolae, hypanthium 0.5 mm. long, perianth lobes ovate, 1–1.5 mm. long and broad, fertile stamens 1 mm. long; fruit ovoid 8–10 mm. long, 6 mm. in diameter; perianth lobes 1–1.5 mm. long in fruit, coronate; achene dark brown.

Distribution: Rare in the Bahamas and Cuba, most abundant in Jamaica and less so in Hispaniola, Puerto Rico, the Virgin Islands, Leeward Islands and Windward Islands south to St. Lucia.

Clarendon: Savoy, *Harris 11639* (C, F, GH, NY, MO, US); Peckham Woods, *Harris 11194* (US, NY); Croft's Mts., *Harris 11219* (F, NY, US). **Hanover:** Quashiba Mt., *Webster & Wilson 5086* (A). **Manchester:** New Green, *Britton 3757* (NY); Mandeville, *Britton 3732* (NY), *3236* (NY). **Portland:** Green Ridge *Eggers 3732* (C); Claverty Cottage, *Harris 5088* (C, US); Mt. Pleasant, Stony Hill, *Harris 11133* (F, NY, US). **St. Andrew:** Long Mt., *Webster 4983* (GH); Hardware Gap near New Castle, *Britton & Hollick 1806* (NY); Clydesdale to Chesterdale, vicinity of Cinchona, *Britton 334* (F, NY); Constant Spring to Bardowie, *Harris 12110* (F, GH, MO, NY, S, US); Port Royal Mts., Content Road, *Harris 5092* (US), *5263* (S, US); Lower Davids Hill, *Harris 5091* (C, US); Liguanea Hills, *Prior s.n.* (NY); Moody's Gap, *Britton 3337* (NY), *3364* (NY); Brandon Hill, *Fawcett 8062* (F, NY). **St. Ann:** Union Hill near Moneaque, *Howard 12031* (GH), *12022* (GH), *12013* (GH), *Prior s.n.* (NY); Mt. Diablo, *Hunnewell 19335* (GH); Lydford P.O., *Howard and Proctor 13536* (A, IJ), *13544* (A, IJ), *14586* (A). **St. Catherine:** Juan de Bolas, *Proctor 7146* (IJ); Holly Mount, *Harris 8901* (NY); Charlton, *Harris 6699* (F, NY); Bogwalk, *Proctor 8185* (IJ). **St. Elizabeth:** Malvern, *Howard & Proctor 13722* (A, IJ), *Britton 1195* (NY); Malvern, Bideford District, *Webster & Proctor 5328* (GH).

St. Thomas: Big Level, John Crow Mts., *Webster & Proctor 5529* (GH); Bath, *Britton 3492* (NY), *Harris 6055* (F, NY); Green Valley, *Harris 5233* (C, NY), *12126* (F, GH, MO, NY, S, US); Mansfield, *Britton 3556* (NY); Blue Mts., *Harris 5274* (US),*5094* (B, BM — TYPE of *C. neglecta*, C, J, US); Without location, *Britton 3656* (NY). **Trelawny:** Oxford, *Britton 430* (NY); Troy, *Britton 919* (NY), *Harris 90994* (F, NY, US), *Howard & Proctor 14119* (A). Parish uncertain: Cedar Hurst, *Harris 5500* (C); "Portland," *Bancroft 11* (US). Without definite location: *Swartz s.n.* (De Candolle Herb., TYPE, S, NY).

COMMON NAME: Wild grape. Collected in flower in July, August and September. Collected in fruit in January, February, March, September and November.

A full discussion of the polymorphic species *Coccoloba swartzii* has been published as the second paper in this series (Jour. Arnold Arb. 37: 317–339. 1956). The Jamaican populations of this taxon are remarkably uniform, although they do grade into the variations found on other islands. The type of the species, a Swartz collection described by Meisner and located in the De Candolle Herbarium, is from Jamaica.

I cannot understand how Fawcett & Rendle, in their comprehensive treatment of the genus for the Flora of Jamaica, overlooked this species and failed to consider it. The specimens recognized here as *Coccoloba swartzii* were called *C. diversifolia* Jacq. in the Flora of Jamaica.

5. **Coccoloba troyana** Urb. Symb. Antill. **6**: 8. 1909; Fawcett & Rendle, Flora Jam. **3**: 116. 1914.

Tree of inland areas, generally on limestone, 7–15 m. tall, commonly branched from the base with several trunks; ultimate branches terete, glabrous with nodes only slightly enlarged; ochreae cylindrical, 10–13 mm. long, glabrous, membranaceous, almost completely deciduous; petioles attached at the base of the ochreae, 1.5–2 cm. long, glabrous; blades cordate-ovate to ovate-elliptic, 7 × 4.5, 8 × 6, 9 × 6, 10.5 × 8 cm. long and broad; apex short acuminate, the base cordate; margin entire, flat, chartaceous, drying buff or tan; midrib and primary veins inconspicuous to prominent on both surfaces, arcuate, anastomosing; primary veins 6–9 pairs, the secondary venation reticulate on both surfaces, glands few, inconspicuous; inflorescence terminal, 5–9 cm. long, generally shorter than the leaves, the rachis glabrous or with glands, the pedicels decurrent so that the axis is angular, ridged and grooved; bracts broadly ovate, less than 1 mm. long, glabrous, the ochreolae membranaceous, to 1 mm. long, pedicels glabrous, at most 1.5 mm. long in fruit; staminate flowers 1–3, the pistillate flowers usually solitary, the hypanthium 1 mm. long, perianth lobes oblong-ovate, 1.5 mm. long and broad, the functional stamens 1.5 mm. long; fruit ovoid, 8 mm. long and 5 mm. in diameter, stalked at the base, becoming fusiform to fusiform-ovoid; perianth lobes appressed, 4–5 mm. long, not coronate; achene chestnut brown, shiny.

DISTRIBUTION: Endemic to Jamaica.

Portland: 2½ mi. SW of Ecclesdown, *Proctor 11375* (IJ). **St. Thomas:** John Crow Mts., *Harris & Britton 10764* (F, NY, US). **Trelawny:** Troy, *Harris 9439* (TYPE B, F, NY, US), *9474* (B, F, NY, US), *10653* (C, F, NY, US), *Britton 600* (F, NY, US), *639* (NY); Ramgoat Cave, *Howard and Proctor 14142* (A), *14383* (A, IJ), *Howard, Proctor & Stearn 14659* (A), *Proctor 10616* (IJ).

Collected in flower in March. Collected in fruit in September and November.

This species is easily recognized even in sterile condition by the cordate leaf shape, the long, pale buff petioles and the buff or tan blades. The angular inflorescence axes with the decurrent pedicels mark the species in flowering and fruiting condition. Despite these apparent characters, the species appears to be very similar to some specimens of *Coccoloba krugii* and it is possible that further collections will show complete transition between the two. Attempts to germinate the seeds of *C. troyana* and *C. krugii* have not been successful and the cytological relationship of these species is not known. There is a possibility that *C. troyana* may be a polyploid race of *C. krugii.*

Urban's original description has not been significantly altered by Fawcett & Rendle. More recent collections show that Urban examined only a fragment of the ochreae and that his report of ochreae 3 mm. long is erroneous.

I have seen a dozen specimens of *C. troyana* in the field between Troy and Kimloss in the Cockpit country. Each specimen was in an isolated and sparsely populated area and was not cut or injured. There were neither trauma-induced adventitious shoots nor spontaneous ones and the nature of the larger leaves generally characteristic of juvenile and fast-growing shoots is not known for this species.

The collection by Harris and Britton from the John Crow Mountains, presumably the southern shoulder of this range, extends the known range of the species in Jamaica from the center at Troy to the opposite and eastern end of the island. The specimens collected by Harris and Britton are in full bud or young flowers and appear to agree in all characters with the more numerous material from Trelawny. More recent collections by Proctor from the John Crow Mountains above Ecclesdown are sterile. I have seen the plants in this area and believe they are correctly assigned here.

6. **Coccoloba krugii** Lindau, Engl. Bot. Jahrb. 13: 145. 1891, Symb. Antill. 1: 222. 1899; Fawcett & Rendle, Flora Jam. 3: 115. 1914.

Coccoloba børgesenii Schmidt, Fedde Repert Sp. Nov. **24**: 75. 1927.
Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Repert Sp. Nov. **24**: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly nodose; ochreae membranaceous, persistent, 3–5 mm. long, petiole attached at the base of the ochreae, 5–6 mm. long; leaf blade ovate, subor-

bicular, 2 × 1.8, 2.5 × 2.5, 4 × 3.5 cm. long and broad, the apex obtuse or rounded, the base cordate or rounded, thin coriaceous, entire, flat or recurved margin, glabrous or rarely with a few hairs near the attachment of the petiole, the midrib flat above, slightly prominent below, the secondary venation minutely reticulate below, smooth above; adventitious shoots with ochreae to 1 cm. long, petioles on shoots to 1 cm. long, the leaf blades generally elliptic, 6 × 4, 7 × 6 cm. long and broad; inflorescence terminal, 5, 6, 8 cm. long, the rachis glabrous, the bracts broadly ovate, membranaceous, less than 1 mm. long, the ochreolae membranaceous, less than 1 mm. long, the pedicels shorter than the ochreolae; pistillate flowers solitary, the staminate flowers 1 or 2 at a node on the axis, hypanthium 1 mm. long, the perianth lobes ovate, 2 mm. long, the fertile stamens 1–1.5 mm. long; fruit ovoid or fusiform, generally 3-angled, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit; achene dark brown.

DISTRIBUTION: Bahamas, Hispaniola, Jamaica, Puerto Rico, the Virgin Islands and some of the Leeward Islands.

Clarendon: Portland Ridge, *Lewis 52* (IJ), *80* (IJ), *Webster 5122* (GH). **St. Andrew:** Lower Valley Cave River, *Proctor 10208* (IJ); Long Mt. on road to Wareka, *Harris 10008* (F, NY, US), *10014* (F, NY, US), *Maxon 10521* (GH, NY, S, US), *Webster 5002* (GH); Long Mt., *Howard 12033* (G), *Webster & Wilson 4861* (GH). **St. Catherine:** Great Goat Island, *Harris 9335* (A, F, NY, US). **St. Elizabeth:** Lovers Leap, Santa Cruz Mts., *Britton 1149* (NY); Yardley Chase, *Harris 9667* (B, F, NY, US); Southfield, *Proctor 11337* (IJ). **St. Thomas:** Albion Mt., *Harris 11690* (F, GH, MO, NY, US), *11681* (F, GH, MO, NY, US). **Trelawny:** Ramgoat Cave, *Howard and Proctor 14395* (A, IJ), *Howard, Proctor & Stearn 14683* (A).

COMMON NAME: Big Family, Crabwood. Collected in flower in July. Collected in fruit in February and March, June, July, August, September and November.

A conspicuous taxon easily recognized in the field and in the herbarium by the ashen gray petioles and ochreae, the yellowish brown or tan leaves and the strongly triangular fruit.

The two Harris collections from Albion Mountain, *11680* and *11681*, were presumably made at the same time and place and probably from adjacent trees which looked different. The second collection consists of specimens distinctly short pilose on all parts and with the leaves rounded and emarginate at the apex. This is the most exaggerated pubescent condition seen in the species, although the same leaf shape has been found with all transitions. The Harris collection from Great Goat Island, *9335*, probably showed the greatest variation in the sheets available for study. Other workers had previously and erroneously labelled several of these sheets *C. pyrifolia*.

7. **Coccoloba tenuifolia** L. Syst. Nat. ed. 10, 1007. 1759, Amoen.

5: 397. 1760, Sp. Pl. ed. 2, 524. 1762; Fawcett & Rendle, Flora Jam. 3: 119. 1914, Jour. Bot. 51: 124. 1913.

Coccoloba leptostachyoides Lindau, Engl. Bot. Jahrb. 13: 207. 1890.
Coccolobis ? frutescens, foliis subrotundis, fructu minore trigone Brown, Hist. Jam. 210, *t. 14, f. 3.* 1756.
Coccoloba excoriata L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Flora Jam. 3: 121. 1914.
Coccoloba bahamensis Britton, Bull. N.Y. Bot. Gard. 4: 116. 1905, as *Coccolobis.*

Shrub, rarely a small tree 6 to 15 feet tall; branches terete, light brown in color, glabrous or puberulent; ochreae membranaceous above and deciduous, coriaceous and persistent below, puberulent; the leaves characteristically borne on lateral shoots and crowded, the petioles short persistently puberulent, 6–9 mm. long, arising from a conspicuous base above the base of the ochreae, the blades generally elliptic, occasionally obovate, oval, oblong or sublanceolate, 3.5 × 2, 7 × 4.5, 8 × 6, 9.5 × 6 to 12 × 10 cm. long and broad, membranaceous to subcoriaceous, the apex acute, short acuminate or rarely obtuse, the base narrowed and unequally rounded to subcordate, the margin entire to undulate, the blade often conspicuously umbonate in the field; midrib and veins flat or impressed above, prominent beneath, primary veins 4–6 pairs, arcuate, the ultimate venations finely reticulate, glabrous above, finely puberulent below, generally tomentose in the axils of the veins and extending on to the lamina persisting or evident as clear hair bases; adventitious shoots with leaves evenly distributed, petioles 2–5 cm. long, the blades 7 × 9 to 18 × 16 cm. long and broad; inflorescence terminal from the lateral leafy shoots, to 8 cm. long, weak and hanging generally strongly curved, the rachis puberulent becoming glabrate; staminate flowers 1–4 at the node, the pistillate flowers usually solitary, bracts broadly ovate, to 0.5 mm. long, the ochreolae membranaceous, 0.5 mm. long, the pedicels 1 mm. long, the hypanthium 1–1.5 mm. long with apparent basal stalk more conspicuous in the pistillate flower, the perianth lobes 1–1.5 mm. long and broad, the functional stamens 1–1.5 mm. long, the functional pistil 1.5 mm. long; fruiting pedicels 1–1.5 mm. long, the fruit ovoid 5–6 mm. long and 4 mm. in diameter with a short stalk 0.5 mm. long, the perianth lobes appressed, the achene tan in color.

DISTRIBUTION: Bahamas, Cuba and Jamaica.

Manchester: Spur Tree Hill, *Britton 1064* (NY), *1665* (NY), Marshall's Pen, *Britton 3706* (NY). **St. Andrew:** Green Valley, *Harris 5391* (US), *12129* (F, GH, MO, NY, S, US); Long Mountain, *Harris 8862* (F, NY, US), *Britton 810* (NY), *Howard 12034* (GH), *12035* (GH), *Webster & Wilson 4880* (A), *4890* (A); Mona, *West & Arnold 559* (GH), Berwick Hill, *Harris 5343* (F, US), *6517* (B, F, NY), *Perkins 1194* (A, GH). **St. Ann:** Falls River, *Harris 5228* (Leiden, US). **St. Elizabeth:** Malvern, *Harris 9808* (F, NY, US); Potsdam, *Britton 1264* (NY); Shooters Hill, *Howard & Proctor 14106* (A); Hampton School, *Webster & Proctor 5307* (GH). **St. Thomas:** Blue Mts., *Harris 5272*

(US); Morant Bay, *Barry s.n.* (IJ). **Clarendon:** Portland Ridge, *Howard 12010* (GH). **Trelawny:** Ramgoat Cave, *Howard & Proctor 14143* (A), *14420* (A). Location uncertain: *March 1989* (TYPE of *C. leptostachyoides*, B, Gott.); *Swartz s.n.* (S), *Hart s.n.* (F, NY). Linnaean Herbarium types of *C. tenuifolia* and *C. excoriata* (Patrick Browne).

COMMON NAME: Wild grape. Collected in flower in July, August, September. Collected in fruit in January, February, August, September, October and November.

Fawcett & Rendle have made the greatest contribution in straightening out the nomenclature of this species which has been confused for many years.

Lindau, the earliest monographer of the genus *Coccoloba*, apparently never saw the specimen of *Coccoloba tenuifolia* L. in the Linnaean Herbarium. Lindau refers only to the description in Linnaeus's Amoenitates Academicae 5 in citing this species in a category of uncertain species (Engl. Bot. Jahrb. **13**: 220. 1890). The Linnaean specimen is in excellent flowering condition and is easily recognized. Lindau, however, described two species from Jamaica, *C. jamaicensis* and *C. leptostachyoides* which Fawcett & Rendle consider identical and synonymous with *C. tenuifolia*. I agree only in part with this conclusion, as I consider *C. jamaicensis*, as based on a March specimen, a hybrid and the same as *C. litoralis* Urban.

There remains one species, *Coccoloba excoriata* L., to be disposed of properly before the terminology of this taxon can be considered stable. Linnaeus based *C. excoriata* on a Patrick Browne specimen which is today in the Linnaean Herbarium. As Fawcett & Rendle report in reviewing this species (Jour. Bot. **51**: 123. 1913 and Flora Jam. **3**: 121. 1914), the specimen labelled *C. excoriata* in Linnaeus's handwriting is a "stout shoot, apparently a young sucker 14 cm. long and 0.5 cm. thick with white bark and brown lenticels; leaves 7.5–10 cm. long, 6–7 cm. broad, broadly elliptical, very shortly acuminate, base sometimes unequal, rounded, nerves on both sides prominulous, veins inconspicuous, dark brown on upper surface, light brown beneath; petioles and ochreae puberulous; ochreae dark brown, broadly tubular, 1 cm. long, permanent base 5–7 cm. long, leaf inserted about the middle of the permanent base."

Fawcett & Rendle sought to identify this species through the common name of "The Mountain Grape Tree" supplied by Patrick Browne and, being unsuccessful, left this taxon as "species insufficiently known" in the Flora of Jamaica. Lindau completely misinterpreted the description and considered *C. excoriata* the same as *C. nivea* Jacquin. He placed the species as a synonym in the section *Campderia*. *Coccoloba nivea* Jacquin is now known as *C. venosa* L. and is a very distinct species.

To identify *C. excoriata* L. it is necessary to consider the adventitious shoots of the common species of *Coccoloba* in Jamaica. I have a collection of such shoots made over a period of five years representing most of the species of the genus known from the island. The specimens which agree most closely with Linnaeus's description and the specimen in the Linnaean Herbarium were collected on Long Mountain just outside of Kingston and

are *Howard 12034, 12035, Britton 810* and *West and Arnold 559.* A Harris specimen, *6517*, from Berwick Hill also matches the sterile Patrick Browne specimen. The vegetation on the dry hillsides of Long Mountain is cut with regularity for fuel and the stumps which produced the adventitious shoots here considered are referable in fertile condition to *C. tenuifolia.* There is no doubt that the Patrick Browne specimen of "The Mountain Grape Tree" and the type of *C. excoriata* is an adventitious shoot of *C. tenuifolia.* Both of these names are published on page 1007 of Linnaeus's Systema Natural. edition 10, in 1759. As the Linnaean specimen of *C. tenuifolia* is an excellent flowering specimen, it is desirable to select this as the type and to consider *C. excoriata* based on a sterile adventitious shoot as a synonym.

Coccoloba tenuifolia is distinctive in having tenuous and characteristically curved inflorescence axes. The clustering of the leaves on short lateral branches gives this taxon a distinctive appearance in the field. The swollen ochreae bases, heavily veined near the attachment of the petiole, are also of diagnostic value.

Anomalies have been seen in this species, also, with fasciated and branched inflorescences relatively common. In one specimen the inflorescence axis is thin at the base, becoming flattened and broad about the middle of its length and dividing into ten branches near the apex. The flowers in the Perkins specimen (*1194*) are monstrous in size and the stamens, numbering from four to seven in various flowers examined, are variously united.

8. **Coccoloba longifolia** Fischer ex Lindau, Engl. Bot. Jahrb. **13**: 161. 1890; Ettingschausen, Denkschriften K. Acad. der Wissenschaften, Vienna **15**: *229, tab. 27, fig. 2.* 1858; Fawcett & Rendle, Flora Jam. **3**: 117. 1914.

Coccoloba venosa Griseb. ex Lindau, Engl. Bot. Jahrb. **13**: 152. 1890, not Linnaeus.
Coccoloba venosa major Lindau, Engl. Bot. Jahrb. **13**: 152. 1890.
Coccoloba rumicifolia Britton, Bull. Torrey Bot. Club **42**: 514. 1915.

Erect shrub, scrambling shrub or tree to 15 m.; branches often scrambling, terete, striate, the nodes not conspicuously swollen; ochreae 4–6 mm. long, obliquely truncate, sparsely to densely short yellow pubescent or glabrate, membranaceous above and evanescent, coriaceous below and persistent, the petiole arising slightly above the base, 14 mm. long, glabrous, puberulent or pilose on the adaxial surface; leaf blades oblong-ovate to sublanceolate-ovate, 7 × 2.5, 8 × 5, 13 × 5, 17 × 7 cm. long and broad, subcoriaceous, glabrous, the margin slightly recurved, the primary veins 6 pairs, arcuate, anastomosing near the margin, the ultimate venation reticulate and evident on both surfaces, the base rounded, cordate or rarely cuneate, the apex obtusely acuminate to long acuminate; adventitious shoots with internodes to 10 cm. in length, ochreae 2.5–3.5 cm. with petiole attached from near the base to about the middle, the petioles to 2.6

cm. in length, the blades ovate, ovate-lanceolate or ovate-elliptic 13 × 9, 21 × 8, 26 × 11, 32 × 12, 40 × 19 cm. long and broad; inflorescence racemose, generally exceeding the leaves, 6, 10, 18, 26 cm. in length, basal ochreae to 6 mm. long, the axis puberulent or glabrate, the bracts triangular, obtuse to 0.5 mm. long, the ochreolae membranaceous generally flaring slightly truncate or obliquely truncate, about 1 mm. long, the pedicels in flower 2 mm. long; staminate flowers 1–4 at each node, the pistillate flowers normally single, rarely 2 at each node, the pedicels and perianth puberulent, the hypanthium campanulate 1–2 mm. long, perianth lobes ovate, generally 2 mm. long and broad; fertile stamens to 2 mm. long; functional pistil 2–3 mm. long; fruiting pedicels 2.5–4 mm. long, fruit bright red, ovoid 10–12 mm. long, 6–7 mm. in diameter, apex slightly turbinate, the base contracted to a short stipe, fruiting perianth conspicuously vascular; achene dark brown or black.

DISTRIBUTION: Endemic to Jamaica.

Clarendon: Leicesterfield, *Harris 10840* (F, GH, NY, US); Peckham Woods, *Harris 10873* (F, GH, NY, US), *11174* (F, MO, NY, US), *12785* (F, MO, NY, US); *Proctor 8227* (IJ). **Hanover:** Kempshot, *Britton 2437* (NY). **Manchester:** Martins Hill near Mandeville, *Harris & Britton 10617* (F, NY, US); New Green near Mandeville, *Harris & Britton 10597* (NY, US), *Harris 6317* (B); Mandeville, *S. Brown 241* (NY). **Portland:** 1.5 mi. SW of Ecclesdown, *Howard, Proctor & Stearn 14778* (A); Swift River District, West Hope Bay, *Harris 6009* (F, NY). **St. Ann:** Union Hill near Moneague, *Britton & Hollick 2736* (NY), *2773* (F, NY), *2777* (NY), *Howard 12029* (GH); Grierfield near Moneague, *Britton 2665* (NY), *2667* (NY); Soho, *Harris 11984* (F, NY, US), *11986* (F, GH, MO, NY, US); Liberty Hill, St. Anns Bay, *Britton 2502* (NY), Mt. Diablo, *Maxon 2219* (NY, US), *Webster & Wilson 5013* (A); Lydford P.O., *Howard & Proctor 13420* (A), *13534* (A), *14579* (A), *Howard, Proctor & Stearn 14600* (A), *Proctor 6397* (IJ), *8642* (A, IJ); Linton Estate near Claremont, *Howard & Proctor 14191* (A); Prickly Pole, *Howard & Proctor 14318* (A). **St. Andrew:** Bogwalk, *Hitchcock s.n.* (MO); Constant Spring, *Campbell 5714* (F, NY). **St. Catherine:** Luidas Vale, *Hunnewell 19334* (GH), *Hunnewell & Griscom 14305* (GH); Hollymount, *Britton 730* (NY), *Harris 6489* (B). **St. Elizabeth:** Pepper, *G.S. Miller 1331* (US); Stanmore Hill, Santa Cruz Mts., *Britton 1308* (NY). **St. Mary:** Gayle, *Proctor 5093* (IJ). **St. Thomas:** John Crow Mts., *Britton 3991* (NY), *Harris & Britton 10689* (F, NY, US), *10758* (F, NY, US), *10756* (F, GH, NY, US); Big Level, *Webster & Proctor 5532* (GH), *5545* (GH); Bath, *Britton 3649* (NY), *Howard, Proctor & Stearn 14808* (A); Bachelors Hill, *Britton 3616* (F, NY); Amity Hall Hill, *Harris & Britton 10716* (F, NY). **Trelawny:** Troy, *Harris 8719* (NY), *8772* (NY); between Troy and Oxford, *Britton 680* (F, NY); Oxford, *Harris 9489* (F, NY); Tyre, *Harris 9462* (F, NY), *Britton 545* (NY); Windsor, *G.S. Miller 1475* (US); Hectors River, *Harris 6005* (B), Troy, *Howard & Proctor 14117* (A); Ramgoat Cave, *Howard & Proctor 14146* (A), *14147* (A), *14153* (A), *14393* (A); Burnt Hill, *Barkley, 22J241* (IJ). **Westmoreland:** Negril, *Britton & Hollick 2034* (NY); Beeston Spring to Bog House, *Webster & Wilson 5032* (A); Teague Gulley, Newmarket, *Britton 1592* (TYPE of *C. rumicifolia*, N.Y.), *Harris 9837* (B, F, NY, US). Locality not certain: *Willdenow 7698* (B); *March 1568* (GH), *674* (Gott.)

Swartz s.n. (S), *Hansen s.n.* (NY), *Prior s.n.* (B, GH, NY). **Cultivated:** Hort. Berlin 1828 (US), 1843(B).

COMMON NAMES: Wild Grape, Bastard Cherry. Collected in flower in March, April, May and July. Collected in fruit in December, February, March, April and May.

Lindau in his monograph of the genus supplies the first complete description of *Coccoloba longifolia* and attributes the name to Fischer. He cites as the first publication of his name the reference "Cat. Pl. Razoum. à Gor. p. 25" and notes that it was without description. I was unable to locate any reference to that publication in the United States and am indebted to the staff of the library at the Royal Botanic Gardens at Kew for their assistance in finding this little book. It is, correctly, "Catalogue du Jardin des Plantes du son excellence Monsieur le comte Alexis de Razoumeffsky a Gorenki." This catalogue was compiled by F. Fischer and was published in Moscow in 1812. The name in question was published in a list on page 16, not 25, as "Coccoloba ? longifolio." It is a nomen nudum. Lindau cites further references for this name, the next being H. F. Link in his Enumeratio Plantarum Horti Regii Botanici Berolinensis 1: 386. 1821, where for the first time the plant is credited to English Gardens. No description is given. Steudel in Nomenclator Botanicus, page 210 in 1821 and again in the 1840 edition on page 290 lists this plant under cultivation as "C. longifolia Fisch." To the latter listing is added the information "Hort. Ang." and "Ind. Occ." and a symbol indicating the species is not well known.

In 1858 C. von Ettingshausen in a preliminary work on the interpretation of fossil plant remains (Denkschriften K. Acad. d. Wiss. Wien. **15**: 229, *tab. 27*, *fig. 2*. 1858) gives a brief description of the vascular pattern of the leaves of "C. longifolia Link" and an illustration. It is obvious that the material he studied originated in the Botanical Garden in Berlin bearing the name from Link's catalogue. It would be permissible, but of doubtful value, to consider the description and illustration of Ettingshausen as the first valid publication of the name *C. longifolia*.

Lindau's complete description has been taken as the starting point for this species by Fawcett & Rendle (Flora Jam. 3: 117. 1914), who refer to *C. longifolia* Fisch. ex Lindau. It would be noted, however, that Fawcett & Rendle literally compile a new description and concept for this species, combining as they do two species and one variety recognized by Lindau in one description. The correct citation for this species should probably be *Coccoloba longifolia* Fisch. ex Lindau emend. Fawcett & Rendle. Lindau recognized *C. venosa* which he attributes to Grisebach. It is based on a manuscript name in the herbarium at Göttingen. Two specimens are cited, *March 674* without locality and an Alexander Prior specimen without number from Moneague. However, *C. venosa* Griseb. ex Lind. is a later homonym for *C. venosa* L. Lindau also described a variety *major* for this species based on another Alexander Prior specimen without location or number. I have seen all three specimens cited in the Grisebach Herbarium at Göttingen. Lindau distinguished this species and its variety from his

newly described "C. longifolia Fisch." as having an inflorescence rachis tomentellose, while *C. longifolia* had the rachis glabrous.

The typification of this species is as difficult as the definition. Lindau cites three specimens from Jamaica, *Cuming 49*, *Purdie* and *Wullschlagel 1389* and a specimen from a locality not indicated on the sheet and collected by "Sivart." This latter specimen according to Lindau is in the herbarium at Leningrad. Although Lindau twice refers to the "Sivart" specimen in his treatments of this species, it seems obvious that this is an error of transcription for "Swartz." One specimen in the herbarium at Stockholm referable to this species bears the annotation "Ind. Occ." and the name "Swartz" written in longhand in such a way that "Sivart" could be implied. Lindau saw this sheet, for it bears his annotation label with the printed date of 1889 and the reference to *Coccoloba longifolia* Fisch. I have seen three of the four specimens cited by Lindau in the first complete description of *C. longifolia*. However, not one of these specimens bears flowers as were described in the original publication of the name. The selection of a lectotype must be deferred until the specimen not seen (*Wullschlagel 1389*) can be located and even then it may be desirable to select a lectotype from a more modern collection.

Fawcett & Rendle broaden the concept of *Coccoloba longifolia* as described by Lindau to include the pubescent forms which Lindau treated as *C. venosa* Griseb. *Coccoloba venosa* var. *major*, the specimens cited by Fawcett & Rendle in the Flora of Jamaica are extremely diverse in the size and shape of the leaves and the amount of pubescence on the stem, ochreae and rachises. Likewise Fawcett & Rendle broaden the concept to allow for more than a single pedicel per node on the inflorescence axis, a character now recognized as sexual. However, since they did not include a discussion, I felt a field study of this species-complex was essential to clarify the differences in these treatments. Between 1950 and 1956 I have had the opportunity of studying *C. longifolia* plants in many parts of Jamaica on five separate trips to the island at different times of the year. Numerous collections were made and cited, but many field observations were not supported with voucher specimens of this relatively common species. I have studied an abundance of living specimens in St. Ann, St. Elizabeth and St. Catherine parishes from near the seacoast at Ocho Rios to altitudes of about 3,000 feet at Griermount. *Coccoloba longifolia* appears to be a weak tree reaching at most a height of 30 feet and occurring often with several erect trunks. The most common occurrence is in cut-over thickets or secondary woodlands. The branches show a tendency toward a scrambling habit. As is true in most species of *Coccoloba*, adventitious branches develop readily following injury and in the case of *C. longifolia*, any distortion of a branch from its normal attitude tends to incite the development of adventitious shoots with longer internodes and larger leaves, petioles and ochreae. As it occurs commonly in disturbed woodlands which are frequently cut for building poles and fire wood, the number of plants with larger leaves considered atypical is greater than the number of plants encountered with smaller and more pubescent leaves and considered

as typical of the species. Collections from the more remote or undisturbed areas of the island of Jamaica tend to exhibit the smaller leaf size and the more abundant phases of pubescence. Thus, collections by Harris (*9462*) and Britton (*545*) from Tyre near Troy in the Cockpit Country, Harris (*12785*) from Peckham Woods and Prior (*s.n.*) from Moneague exhibit what Lindau considered as *C. venosa* Griseb. var. *typica*. It is interesting that an older collection by A. S. Hitchcock (Dec. 17, 1890) from Bogwalk, an historic location, shows the same characteristics, but has never been re-collected in this area. Of the many living plants of this species seen along the gorge of the Rio Cobre below Bogwalk, all illustrate the more rampant growth form. I likewise revisited the Moneague area, particularly Union Hill, where Britton and Hollick (*2773*) in 1908 collected the same growth form of *C. longifolia* as did Prior. In the protected forested area I was able to find specimens which duplicated the earlier collections, but at the edge of clearings and in areas of regrowth the full range of variation was found, from small and pubescent leaves with short inflorescences to large and essentially glabrous leaves with long inflorescences. These variations were found on many occasions and often on one plant (*Howard 12029*, GH). The most striking contrast on one tree was found in the Claremont area of St. Ann, where specimens were made (*Howard 14191*, A) of a single tree which had one shoot showing normal growth form and many adventitious shoots from the base and from stumps of other branches, showing the full range of variation.

One can conclude from a careful field study that *C. longifolia* is a common species showing considerable variation in leaf size, shape, texture and venation pattern and in the length, thickness and pubescence of the inflorescence, as well as the length of the pedicels. Anomalous inflorescence axes are to be expected in this species, for field study showed elephantine development producing rachises which were longer than the leaf and which, on drying, were 5–7 mm. thick while on the same branch another inflorescence axis might be ¼ to ¾ the length of the leaves, but extremely thin and delicate. Several of the thicker inflorescence axes were branched at the apex, as in *Harris 9489*, indicating a teratological development.

Coccoloba rumicifolia described by Britton and based on a collection (*1592*) he made while collecting with Harris (*9837*) at Teague Gulley near New Market (published incorrectly as "Tea Gulley") represents the more fragile aspect of *C. longifolia*. The plants, described by Britton as three meters tall and growing on a wooded hillside, have membranaceous leaves as well as weak, short inflorescence axes with short pedicels. There is no doubt that this species should be referred to the synonymy of *C. longifolia*.

There remains some question as to why this species was in cultivation in the gardens and greenhouses of Europe in the early nineteenth century. Certainly the plant does not have the horticultural possibilities of *Coccoloba uvifera*, *C. rugosa* or *C. pubescens* which were in cultivation at the same time. The oldest horticultural herbarium specimen known to me is currently in the U.S. National Herbarium (*617174*). This specimen is labelled

"*Coccoloba longifolia* Hort. Angl." and "ex. hort. bot. berol. 1828", thus agreeing with the citation of Link's catalogue of 1821. The erroneous annotation "28 Cocc. caracasana Meisn." in an unidentified handwriting is also on the label. The specimen was sent from the Botanic Garden at Berlin to the Herbarium of the Bureau of Science in Manila and eventually was transferred to the U.S. National Herbarium. It is interesting to note that this specimen bears Lindau's annotation label of 1889. In the herbarium of the Berlin Botanical Garden there is another specimen apparently cultivated under the name of *Coccoloba barbadensis* which was growing in the garden at Berlin in May 1843. This specimen was annotated by Lindau as *C. longifolia.* There is also a specimen of *C. longifolia* in the Kew Herbarium bearing the information, "Hort. Kew 1857." Although Lindau annotated all of these sheets, he did not cite them in his monographic treatments of the genus. All three specimens represent the fast-growing aspect of the species with larger, thin leaves and long, slightly puberulent rachises. All are pistillate specimens, raising the question of how these early cultigens were propagated if they did not all come from the same seed lot. If the latter is true and these were all one seed collection, then further unanswered questions are raised regarding the inheritance of sex in these dioecious plants.

9. **Coccoloba diversifolia** Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114, *pl. 76.* 1763; Howard, Jour. Arnold Arb. **30**: 421. 1949.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13**: 158. 1891, Urban, Symb. Antill. **1**: 227. 1901; Fawcett & Rendle, Flora Jam. **3**: 116. 1914 and all recent authors, not Jacquin.
Coccoloba longifolia Schmidt, Fedde Rep. Sp. Nov. **24**: 73. 1927, not Fischer.
Guaiabara laurifolia House, Am. Midl. Nat. **8**: 64. 1922 (as Guaibara).

Shrub or small tree to 7 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly tumid; ochreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; petioles 7–10 mm. long, glabrous; leaf blades ovate, oblong, elliptic, lanceolate or obovate, variable on a single shoot, the apex rounded, obtuse, acute or acuminate, the base cuneate to rounded or subcordate, 4 × 3.5, 7 × 5.5, 8× 4.5, 12 × 8 cm. long and wide, coriaceous, often shining above, dull beneath, glabrous, the midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin, the margin entire, commonly slightly recurved; leaves of adventitious shoots similar in shape to those of normal growth but larger in size, 17 × 8, 24 × 13, 32 × 12.5 cm. long and wide on petioles 1–2.5 cm. long; leaves of windswept specimens often much smaller than those of normal shoots, 2 × 1.3, 3 × 2 cm. long and wide; inflorescence terminal 4.9, 9, 11 to 18 cm. long; rachis glabrous; staminate flowers in clusters of 2–5, the pistillate flowers solitary; bracts ovate, less than 0.5 mm. long, 1 mm. broad, glabrous; ochreolae membranaceous, less than 0.5 mm. long, glabrous, the

flowering pedicels 2–4 mm. long, glabrous; hypanthium 1 mm. long, the perianth lobes 2 × 2, to 3 × 1 mm. long and broad, filaments of functional stamens 1 mm. long, fruiting pedicels 3–4.5 mm. long; fruit globose to obpyriform 10 × 7, 12 × 8, 13 × 8 cm. long and thick, perianth lobes appressed at the apex of the achene.

DISTRIBUTION: Florida and the Bahamas, through the West Indies to South America.

Clarendon: Portland Ridge, *Howard 12004* (GH). **St. Andrew:** Gordon Town, *Harris 6032* (F, NY, US). **St. Elizabeth:** Pepper, *G.S. Miller 1354* (US), *1365* (US); Malvern, *Howard & Proctor 13689* (A, IJ), *13724* (A, IJ); Gutters, *Howard & Proctor 13821* (A, IJ). **St. Thomas:** Sheldon, *Harris 5093* (US).

Collected in flower in July and in fruit in February and November. This species, particularly abundant in the Bahamas, Cuba and Hispaniola, is of infrequent occurrence in Jamaica. It is apparently limited to the south coast and specimens were not abundant in the one region, Portland Ridge, where I have collected it. The plant was not known to others of our party and no common name was offered by the residents of the area.

10. **Coccoloba zebra** Griseb., Fl. Brit. W.I. 162. 1859; Lindau, Engl. Bot. Jahrb. **13**: 135. 1890, Symb. Antill. **1**: 220. 1899; Fawcett & Rendle, Flora Jam. **3**: 113. 1914.

Coccoloba harrisii Lindau, Urb. Symb. Antill. **1**: 228. 1899; Fawcett & Rendle, Flora Jam. **3**: 117. 1914.
Coccoloba priorii Fawcett & Rendle, Jour. Bot. **51**: 124. 1913, Flora Jam. **3**: 120. 1914.

Tree to 30 feet tall; branches terete, slender, glabrous; ochreae subcoriaceous, persistent, slender and cylindrical but flaring and oblique at the apex, 8–14 mm. long, glabrous; petiole attached at the base of the ochreae, slender, 11–14 mm. long on normal shoots, glabrous; leaf blades elliptic to elliptic-ovate, 7 × 4, 8 × 6, 10 × 7 cm. long and broad, coriaceous, glabrous, flat, dull turning black on drying, the midrib and primary veins flat above, prominent below, the veins 5–7 pairs, arcuate, anastomosing, the secondary venation densely reticulate, the apex short acuminate, the base rounded to truncate; leaves of adventitious shoots similar in shape, 15 × 9 cm. long and broad on petioles to 2.4 cm. long; inflorescence terminal 5–14 cm. long, the ochreae of rachis flaring, 8 mm. long, puberulent, the rachis puberulent; bracts and ochreolae less than 0.5 mm. long, glabrous or puberulent, the pedicels 1.5–2.5 mm. long, puberulent, the pistillate flowers borne singly, the perianth puberulent, the hypanthium 1.5 mm. long, the perianth lobes 1.5 mm. long and broad, the stamens rudimentary, the pistil 1.5 mm. long; staminate flowers not known; fruiting pedicels 3–4 mm. long; fruit fusiform, 17 mm. long, 8 mm. in diameter; perianth fibrous; achene dark brown.

DISTRIBUTION: Endemic to Jamaica.

St. Ann: Union Hill near Moneague, *Prior 338* (K, TYPE of *C. priorii*, B). **Manchester:** below St. Georges, *Watt s.n.* (NY). **Portland:** 2.5 mi. SW of Ecclesdown, *Howard, Proctor & Stearn 14754* (A); *Webster & Wilson 5133* (A); *Proctor 11371* (IJ); Vinegar Hill, *Harris 5481* (C, BM, TYPE of *C. harrisii*), *7667* (B, BM, F, NY, US). Parish not certain: Blue Mts., *Harris 5089* (B, BM). Locality not certain: *Wilson 168* (Gott. TYPE of *C. zebra*, B, K); *March 679* (Gott.)

COMMON NAME: Zebra wood (ex Grisebach). Collected in flower in July and September. Fruiting date not known. The type specimen of *Coccoloba zebra* is a fruiting branch of a vigorous shoot. The internodes are long and the leaves larger than in the other collections cited. The type specimens of *C. harrisii* and *C. priorii* are shoots of normal growth. It is clear to me that these collections represent one taxon and that *C. zebra*, being the older name, must be used. Lindau distinguished *C. harrisii* from *C. zebra* primarily on the assumption that *C. harrisii* had a glabrous rachis. I have seen all the material Lindau cited and annotated and conclude he was in error on this point.

Fawcett & Rendle do not discuss their new species *C. priorii* in the original description, but in the Flora of Jamaica they distinguish it from *C. harrisii* as having "veins on the upper surface only seen with a lens when dry" while *C. harrisii* has "veins on the upper surface evident." These two species form a section of the key headed "leaves small, not exceeding 8 cm." while *C. zebra* is distinguishable from this section by having "leaves large, exceeding 8 cm." These are not reliable characters.

The specimens cited from the crest of the John Crow Mountains near Ecclesdown represent an extension of the range of the species and unfortunately are sterile. However, the vigorous and normal growth aspects of these bridge the variation expressed in the earlier collections. *Coccoloba zebra* is not adequately known and additional material is needed. Only one fruiting specimen is known and this consists of very old fruit. The fruits are all detached and are in a pocket on the sheet. If the fruits belong with the vegetative parts, the shape of the fruit is an additional diagnostic character for the species. Staminate plants or flowers with functional anthers have not been seen. The specimens recently collected are the only modern collections and as this location is known to botanists in Jamaica, it is hoped that the additional characters can soon be added to this description.

HYBRIDS AND SPECIES EXCLUDED FROM THE FLORA OF JAMAICA

Coccoloba × jamaicensis Lindau (stat. nov.) Engler Bot. Jahrb. 13: 206. 1890, Symb. Antill. 1: 232. 1899.

Coccoloba litoralis Urban, Symb. Antill. 6: 9. 1909; Fawcett & Rendle, Flora Jam. 3: 117. 1914.

Coccoloba leoganensis Griseb. ex Lindau Engl. Bot. Jahrb. 13: 206. 1890, not Jacquin.

Tree to 13 m. tall; branches terete glabrous, the nodes not conspicuously enlarged; ochreae subcoriaceous, glabrous or with minute puberulence, persistent, the apex oblique, 6–9 mm. long; petiole inserted above the base, stout, 1.5 cm. long, glabrous or minutely puberulent; leaf blades broadly orbicular-ovate, 7 × 6, 11 × 9, 15 × 11, 16 × 12 cm. long and broad, the apex acute or rounded and slightly mucronate; the base rounded to cordate, thin coriaceous, glabrous, sunken glands sparsely distributed above, dense below, these black when dry, the midrib and primary veins prominent on both surfaces, primary veins 5–6 pairs, arcuate, anastomosing, ultimate venation minutely and densely reticulate; margin undulate to entire and flat; inflorescence terminal, solitary or with reduced inflorescence at the base, 12, 18, 35 cm. long, the axis puberulent, the bracts ovate above, 1 mm. long, the ochreolae 1 mm. long, both puberulent, the pedicels 1–1.1 mm. long in flowering condition; staminate flowers 2–4 per node, the pistillate flowers solitary, the hypanthium 1–1.5 mm. long, the perianth lobes 1.5–2 mm. long and broad, the fertile stamens 1.5 mm. long; fruits immature and abortive, stalked and similar in size and shape to those of *C. uvifera*.

DISTRIBUTION: Endemic to Jamaica.

St. Catherine: Great Salt Pond, *C. B. Lewis s.n.* (IJ 3231). **St. Elizabeth:** Slipe district, 2–4 mi. SW of Lacovia, *Howard & Proctor 14509* (A), *14512* (A); 1.5 mi. N of Fullerwood in Black River Swamp, *Howard & Proctor 14508* (A). **Westmoreland:** Negril, *Harris 10228* (B, TYPE of *C. litoralis*, BM, F, N.Y. US), *Britton & Hollick 2057* (NY). Locality uncertain: *March s.n.* (Gott., TYPE, B, GH).

Unfortunately considerable shifting and re-sorting of names is required to establish the correct epithet for this taxon which is now recognized as a hybrid. *Coccoloba jamaicensis* was described by Lindau and one collection, March without number, was cited. Lindau saw two specimens, one in the Grisebach Herbarium at Göttingen and the other in the Krug & Urban herbarium in Berlin. Both of these collections are fragmentary, with the specimen in the Krug & Urban herbarium consisting of one leaf and two pencil tracings. A third specimen of this collection has been found in the Gray Herbarium and is more complete and in better condition than either of the others. After careful comparison of these three collections, I have no doubt of their origin from the same plant. They represent a flowering branch with relatively young leaves.

In his original monograph of the genus *Coccoloba* Lindau was unable to identify *C. tenuifolia* L. and listed this species in a category of uncertainty at the end of his publication. He did describe *C. jamaicensis* and *C. leptostachyoides*, the latter based on a numbered March collection from Jamaica. In a treatment of *Coccoloba* in the West Indies published in 1899 in Symbolae Antillanae, Lindau concluded that his species *C. leptostachyoides*

was the same as his *C. jamaicensis* and listed the former in synonymy. Fawcett & Rendle, in studying the Linnaean species of *Coccoloba* from Jamaica, recognized that *C. tenuifolia* L. "is the species which has been recently described by Lindau as *C. jamaicensis* in Engl. Bot. Jahrb. xiii. 206. 1890." This is the treatment which Fawcett & Rendle published in the Flora of Jamaica and which I followed in a treatment of the genus *Coccoloba* in Cuba (Jour. Arnold Arb. 30: 407. 1949). After having studied the March collection which is the type of *Coccoloba jamaicensis* and having compared it with the March collection *1989*, the type of *C. leptostachyoides*, and the Browne collection in the Linnaean Herbarium, the type of *C. tenuifolia* L., I find it necessary to agree with Lindau that two taxa are represented in the two March collections. *Coccoloba tenuifolia* L. is the same as *C. leptostachyoides* Lindau. *Coccoloba jamaicensis* Lindau, however, based on the March collections cited, is different from *C. tenuifolia* L., but is the same as the material currently recognized as *C. litoralis* Urban.

Coccoloba litoralis as described by Urban was based on specimens collected by Harris at Negril. Harris reported the plant as a tree of 40 feet growing near the rocky seacoast among coconut plantings. Urban's observations compared this new species with *C. polystachya* of South America, *C. laurifolia* Jacq. and *C. verruculosa* of Hispaniola. It is clear after examining the specimens which Urban had for study in Berlin and additional specimens in the field that *C. litoralis* is a hybrid between *C. uvifera*, the common sea grape, and *C. tenuifolia* of the dry coastal areas of Jamaica.

The specimen by Britton & Hollick was collected on the same area, Negril, from the same size tree and in the same condition, during the same period. It is suspected that Britton & Hollick were with Harris on this day and that their collection is from the same tree as the Harris specimen, the type of *C. litoralis*.

In July of 1955 Mr. George Proctor and I had opportunity of collecting in the Black River Swamp area of southern St. Elizabeth parish. Where the one road crosses the Broad River there was a well developed stand of *C. uvifera* of characteristic appearance and scattered among them were trees noticeably different to one familiar with the sea grape. Five or six of these trees were seen, the largest being 25 feet tall. All had the general sprawling habit of the sea grape, but differed in having generally smaller and thinner leaves much more green in color. The inflorescences of these plants were long and tenuous and generally weak and drooping. Both staminate and pistillate plants were seen in flower, but all fruits were either abortive or immature. In fact, the largest fruits seen were on staminate inflorescences and all of these fruits were hollow and obviously sterile. One collection in the herbarium of the Arnold Arboretum (*Howard & Proctor 14509*) was deliberately prepared to show the variation possible on one tree. The branches were selected and mounted to show specimens that looked as much like *C. tenuifolia* and as much like *C. uvifera* as possible. In fact, the specimen cited would key out to *C. tenuifolia* or *C. uvifera* in the key given, but would look unlike the species. Most of

the plants possessed conspicuous adventitious shoots and these and their leaves were thinner in aspect than is typical for *C. uvifera*. Closer study of the herbarium specimens prepared indicates that these specimens are identical with those named *C. litoralis* by Urban. It is clear from field observation of the living plants and from study of the specimens prepared that *C. litoralis* is a hybrid between *C. uvifera* and *C. tenuifolia* and that the correct name for this taxon is *C.* × *jamaicensis* Lind. No specimens of *C. tenuifolia* have been collected from the immediate vicinity of the plants seen in the Black River swamp, although this species was observed about 4 miles away on dry hummocks in the same swamp.

Several populations of hybrids involving *C. uvifera* as one parent are known from the Antilles. In all cases the characteristics of *C. uvifera* dominate those of the other parent in appearance, both of the plant, the habit and the leaves. The inflorescence character, as is the case in *C. litoralis*, is that of the other parent. The fruit in all of the hybrids observed have been sterile, but the specimens seen in the field are relatively numerous. It appears that *C. uvifera* is receptive to cross pollination from other species of *Coccoloba*, but there is some genetic disturbance preventing the formation of fertile fruits and viable embryos.

COCCOLOBA PYRIFOLIA Desf., Fawcett & Rendle, Flora Jam. 3: 114. 1914 (as *C. pirifolia*).

Lindau (Symb. Antill. 1: 222. 1899) refers a Wilson specimen from Jamaica to this species. No locality is known for this specimen. Fawcett & Rendle cite two specimens from the Great Valley in the parish of Manchester collected by Purdie and by Wilson. I cannot determine whether Lindau and Fawcett & Rendle refer to the same Wilson collection. Both George Proctor of the Institute of Jamaica and I have searched and collected extensively in this area and have found only *Coccoloba krugii* in the region. After the publication of the treatment of the genus *Coccoloba* in the Flora of Jamaica, Harris collected additional material which has been referred to *C. pyrifolia*. All such specimens that I have seen from Jamaica I believe to be identified incorrectly and should be referred to *C. krugii*. It seems probable that the Purdie and Wilson collections may also prove to be from adventitious shoots of *C. krugii*. At the present time *Coccoloba pyrifolia* is not known from Jamaica.

COCCOLOBA PUBESCENS L., Fawcett & Rendle, Jour. Bot. 51: 123. 1913, Flora Jam. 3: 118. 1914.

This is a common species of eastern Hispaniola, Puerto Rico and islands of the Lesser Antilles. There are no modern records of this plant from Jamaica. Fawcett & Rendle reported seeing a Wright specimen which I was not able to locate at the British Museum. They also emphasize the fact that Patrick Browne reported this species as common between Kingston and Bull Bay. Browne commented that the plants were of low size, seldom rising above 5 or 6 feet. The area between Kingston and Bull Bay,

while populated and subject to heavy traffic, has not been drastically altered by man for cultivation because of the extreme dry conditions prevalent. *Coccoloba pubescens* in adventitious growth is not one of the better woods and it is difficult to believe that the species, if it occurred there, could have been exterminated either by cultivation or by use. I feel that there is an error in ascribing *C. pubescens* to the flora of Jamaica.

COCCOLOBA VENOSA L., Fawcett & Rendle, Jour. Bot. **51**: 123. 1913, Flora Jam. **3**: 120. 1914.

It is acknowledged in the Flora of Jamaica that no specimens of this plant have been reported from Jamaica since the time of Browne and Swartz. The Browne diagnosis, based on a Plukenet description and drawing, is the basis of this report, as well as a great deal of confusion in the genus *Coccoloba*. The Plukenet material, preserved in the Sloane Herbarium at the British Museum, is the same as *C. nivea* Jacq. and *C. venosa* L. A fruit cluster illustrated by Plukenet is the basis for the epithet "punctata" later applied to the species by Linnaeus. (This was used by Lindau in Symbolae Antill. 1: 228. 1899.) The fruit does not belong with the foliage, is not that of *Coccoloba* and has not been preserved with the leaves. I have not found material in the Swartz herbarium which could be attributed to Jamaica and I believe the ancient report of this species from Jamaica, unsupported by more recent collections, is in error and that *Coccoloba venosa* L. should be deleted from the list of species found in Jamaica.

COCCOLOBA NIGRA, Fawcett & Rendle, Jour. Bot. **51**: 124. 1913; Flora Jam. **3**: 121. 1914.

The type of this species is in the herbarium at the Royal Botanic Garden, Edinburgh and, as reported by Fawcett & Rendle, bears only the annotation "Jamaica" without the collector's name or other data. I have examined this specimen and conclude that it did not come from Jamaica. In fact, it appears certain to be part of a collection by Schomburgk (*531*) collected in the Guianas in 1838, which is the type collection of *Coccoloba ovata* Benth. The Schomburgk collection is also represented in the Edinburgh herbarium and the type of *Coccoloba nigra* appears to match the Schomburgk material even to the foliose lichens on the stem. This species should not be recognized from Jamaica.

COCCOLOBA EXCORIATA L., Fawcett & Rendle, Jour. Bot. **51**: 123. 1913, Flora Jam. **3**: 121. 1914.

This species is referable to *Coccoloba tenuifolia* L. and is discussed under the latter species.

COCCOLOBA RUMICIFOLIA Britton, Bull. Torrey Bot. Club **42**: 514. 1915.

This is the only species attributed to Jamaica described since the publication of the Flora of Jamaica and this I refer to synonymy and discussion under *C. longifolia* Fisch. ex Lindau.

THE NODAL ANATOMY AND THE PRIMARY VASCULAR CYLINDER OF THE CALYCANTHACEAE

Abraham Fahn and I. W. Bailey

With two plates

The vascular anatomy of the Calycanthaceae has long been known to be of a peculiar character, owing to the presence in the internodes of most stems of four [1] inverted "cortical" vascular bundles. These bundles [2] which first appear in the epicotyl of the seedling extend throughout the stems of mature plants and have branches which enter the opposite leaves at the nodes.

In the past, investigators in studying the anatomy of the stem have focused their attention largely upon the structure and behavior of the aberrant cortical bundles.[3] Less attention has been given to tracing the course of the strands in the normal part of the eustele. There is evidence in some dicotyledons which may be interpreted as indicating the derivation of cortical bundles by modification of the lateral traces of plants having trilacunar or multilacunar nodes. It is important in studying the relationships of the Calycanthaceae to determine whether the cortical bundles of the family have evolved in this way or have developed by the addition of a superimposed system of vasculature in plants having fundamentally unilacunar nodal structure. In this connection we have made a detailed investigation of the primary vascular cylinder of the Calycanthaceae which we report in the following pages.

MATERIAL AND METHODS

Material of both *Calycanthus* and *Chimonanthus* was examined. Branches of *Calycanthus fertilis* Walt. (*C. glaucus* Willd.), Arnold Arboretum 12946, *C. fertilis* Walt. var. *laevigata* (Willd.) Bean (*C. fertilis* var. *ferax* (Michx.) Rehd.) A. A. 13400, *C. floridus* L., A. A. 5255 and *C. floridus* L. var. *ovatus* (Ait.) D.C., A. A. 1542 were obtained from shrubs growing at the Arnold Arboretum. Branches of *Chimonanthus praecox* (L.) Link. (*C. fragrans* Lindl.) were secured from the garden of Dr. H. L. Blomquist, Durham, N. C.

The youngest parts of the growing shoots — the vascular system of which consisted of primary tissue only — were cleared by heating in lactic acid, and were examined, after removal of the hairy epidermis, while

[1] Baillon (3) refers to the occurrence of five such bundles in a specimen of *Chimonanthus fragrans* (= **C. praecox**). This rapidly elongating specimen had a 2/5, instead of the usual decussate, phyllotaxis.

[2] Van Tieghem (13) claimed that they develop in the pericyclic tissue of *Chimonanthus*.

[3] In this connection see Baillon (3), Boureau (4), Lignier (6), Quinlan (10), Tieghem (13), Woronin (14) and Worsdell (15).

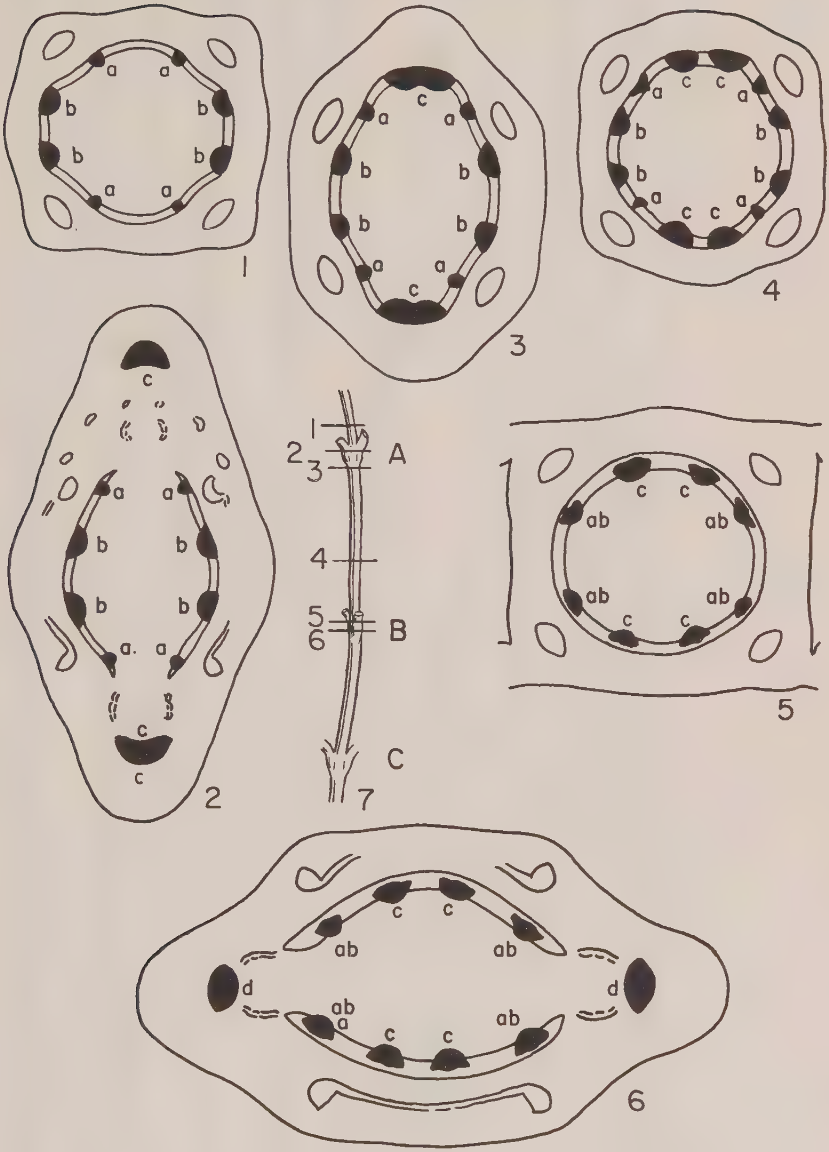
preserved in the acid. In some cases, it was necessary to treat the cleared material for about 20 minutes with a 10% solution of sodium hydroxide in order to remove crystals which appeared after clearing with lactic acid. In addition, the terminal parts of growing stems were embedded in paraffin and serially sectioned through 3–4 nodes from the apex downward. These serial transverse sections were stained with safranin and fast green. Parts of branches having secondary vascular tissues were serially cross-sectioned through three nodes. The sections were made from living stems with a sliding microtome without embedding. They were arranged serially on slides in glycerine mounts.

OBSERVATIONS

The primary vascular pattern in the stems of the species examined was found to be basically the same in both genera of the Calycanthaceae. The chief differences observed were in the levels of "branching" and "fusing" of the vascular bundles of the eustele. In both genera, it was possible to follow successive stages in the "fusing" of pairs of leaf traces during the development of the unilacunar nodes and during the elongation of the internodes.

In the terminal parts of cleared growing shoots, *Plate I, A & B*, the developing leaf traces reveal no appearance of approximation or fusing below the levels of attachment of the leaves. In serial cross sections of such immature parts of the stems, there are two discrete strands of xylem and phloem. No procambial tissue could be detected between them, indicating that two independent strands of procambium develop at an early stage. At lower, more laterally expanded levels of the shoot, *Plate I, B*, approximation of the vascular strands of each foliar pair is attained by the downward extension of additional longitudinal files of tracheary cells. This appearance of ontogenetic fusing is obvious in comparing successively formed pairs of leaf traces in the same orthostichy of the decussate phyllotaxis. Each trace of a foliar pair also fuses with a trace of another leaf, approximately two nodes below the level of the leaf which it vascularizes, *Plate I, B*.

In serial cross sections of older parts of the stem, the existence of a similar pattern of primary vasculature may be traced. For example in cross sections of *Calycanthus fertilis* var. *laevigatus*, *Fig. 7*, there are eight primary bundles in the eustele just above the level of node A, *Fig. 1*; two pairs of traces labeled (a) and two pairs marked (b). At the nodal level of A, there are two additional large vascular strands (c) located opposite two conspicuous gaps in the eustele, *Fig. 2*. Just below the nodal level of A, these strands (c) form integral parts of the eustele, *Fig. 3*, which now consists of 10 traces. Lower in the internode the inherent doubleness of strands (c) becomes increasingly apparent, *Fig. 4*, and there are 12 well separated traces. At the base of the internode, *Fig. 5*, the number of discrete strands is reduced to eight by the approximation or "fusion" of four pairs of the (a) and (b) strands. At node B, *Fig.* 6, the arrangement



FIGURES 1–6. Cross sections of the mature part of a shoot of *Calycanthus fertilis* var. *laevigatus*, cut at the successive levels shown in FIGURE 7. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

described at node A recurs except that the axis of the leaf gaps is now at right angles to that at node A.

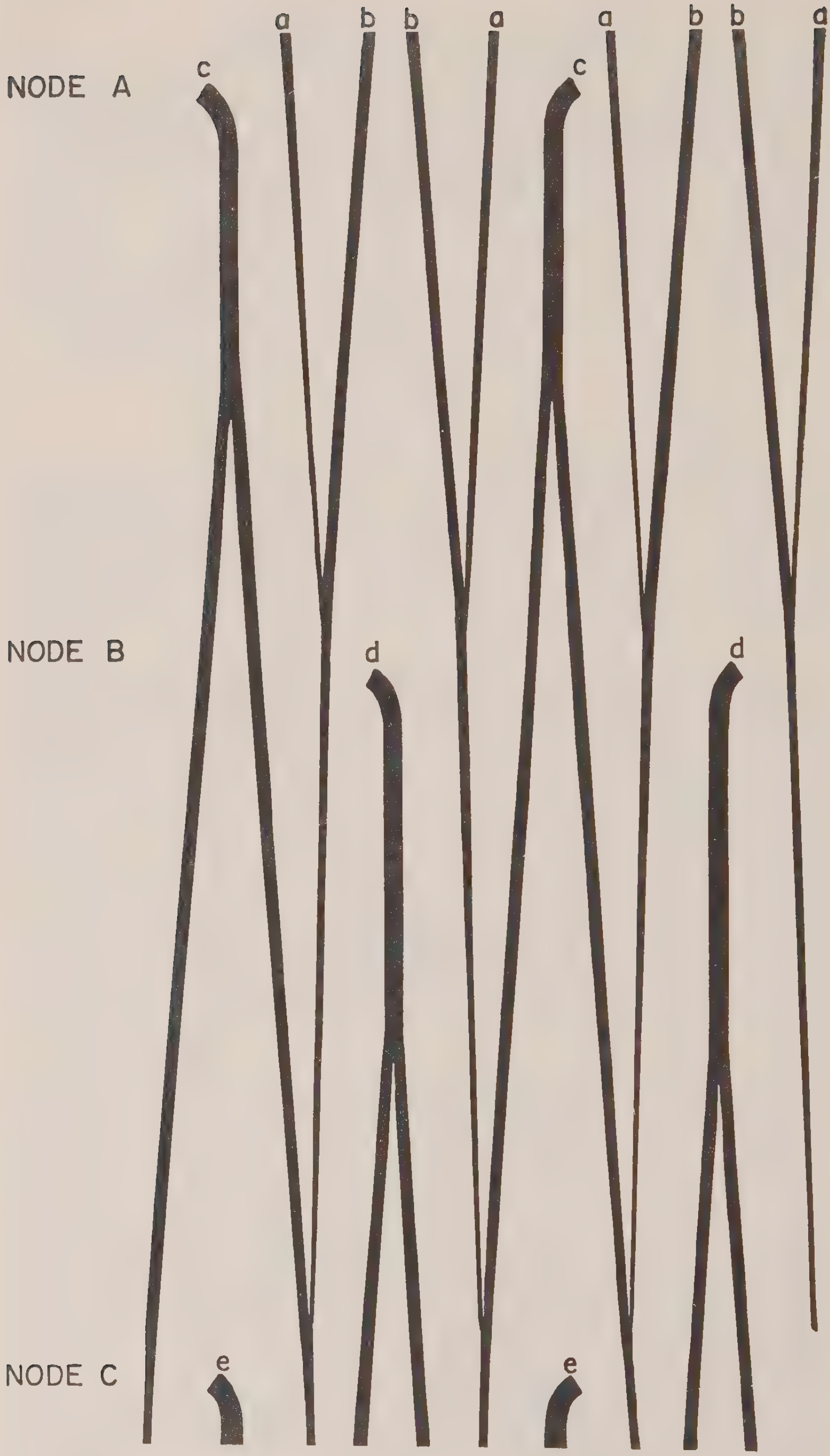


FIGURE 8. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus fertilis* var. *laevigatus*.

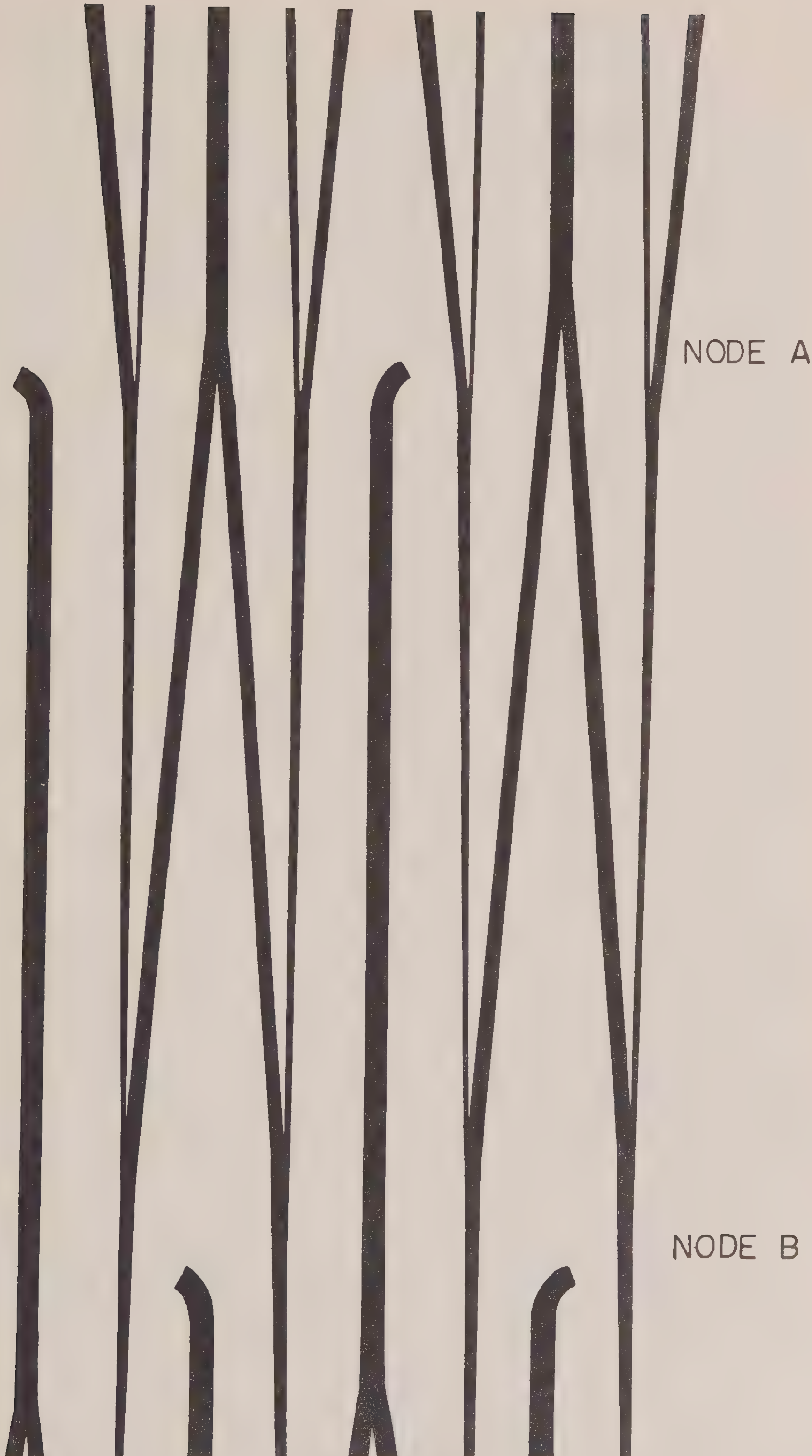


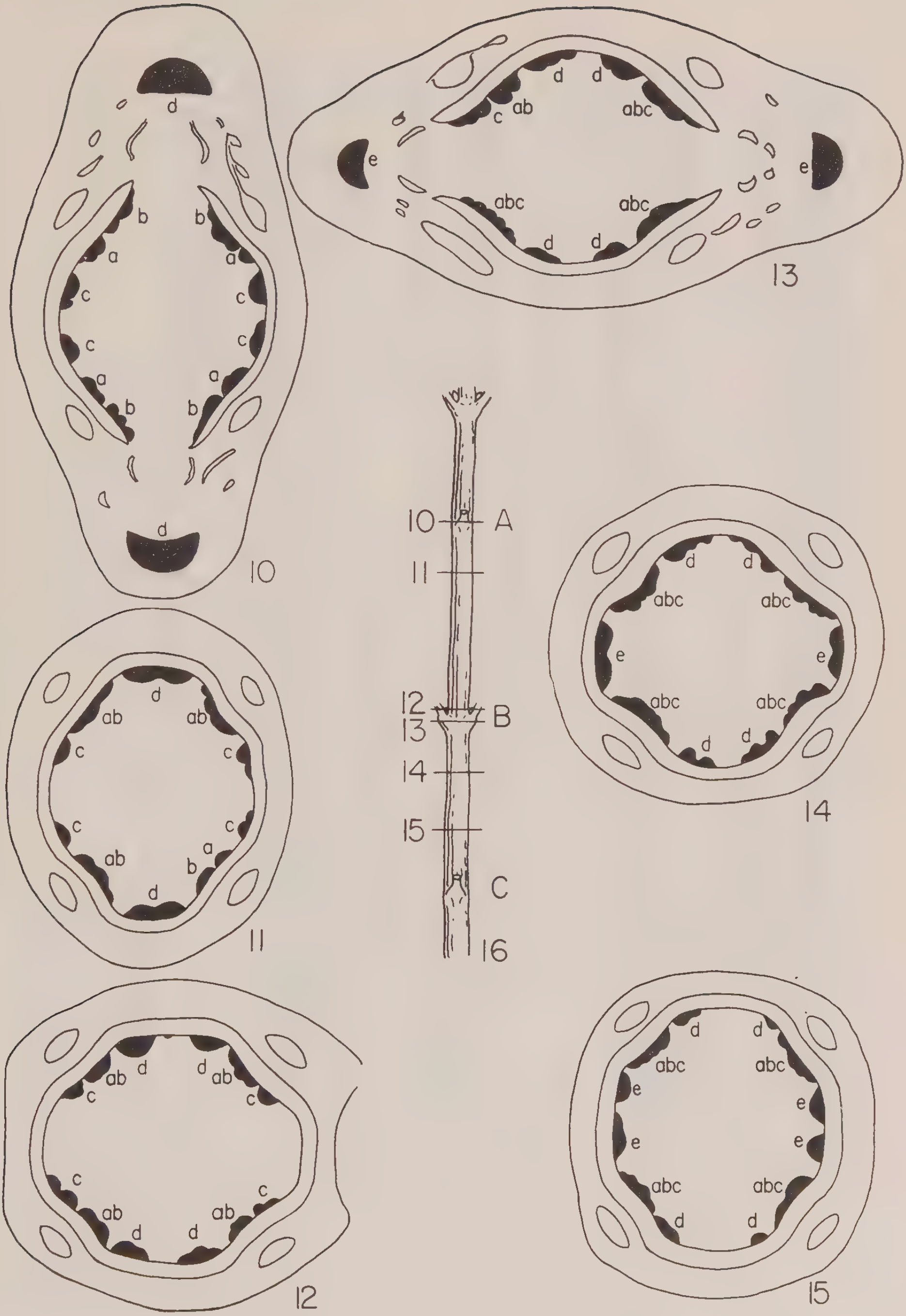
FIGURE 9. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus floridus* var. *ovatus*.

The longitudinal course of the leaf traces in the mature stem may be reconstructed from serial cross sections, and is diagrammatically shown in *Fig. 8*. The pattern is in agreement with ontogenetic evidence obtained from the elongating, immature, terminal parts of the axis, *Plate I, B*.

In fully matured stems, the paired leaf traces commonly approximate or apparently "fuse" in the middle part of the first subtending internode below the level of attachment of a leaf. In early ontogenetic stages, the fusing of the two principal foliar strands, as previously mentioned, occurs only within the leaf itself, *Plate I, B*.

As in the case of *Austrobaileya*, *Trimenia*, *Ascarina* and other plants having fundamentally double-trace unilacunar nodes, there is considerable individual and interspecific variation in the levels at which fusing of the two leaf traces occurs and in the levels at which these traces join the traces of other leaves, compare *Figs. 8 and 9*. Thus, the number of discrete strands visible in cross sections of mature stems varies at times even at corresponding levels. For example, as shown in *Fig. 8*, there commonly are in stems of *Calycanthus fertilis* eight bundles in cross sections cut immediately above the node, twelve bundles at a slightly higher level and ten strands in the upper part of the internode. In branches of *Calycanthus floridus* and in some stems of *C. fertilis*, the number of vascular strands differ from this at corresponding levels. For instance, in *Fig. 9*, there are only six bundles immediately above node B and eight strands immediately below it. In some stems there may be as many as fourteen discrete strands at certain levels. In this connection, it is desirable to consider the effects of variations in internodal elongation.

In branches of *Chimonanthus praecox*, obtained through the courtesy of Dr. Blomquist, the primary vascular bundles, as seen in transverse sections, are relatively broad and the interfascicular spaces of the eustele are comparatively very narrow. This feature develops very early in the ontogeny of the axis, *Plate II, B*. It makes it difficult at times to follow the course of individual traces during later stages of the maturation of the stem. However, careful analysis of serial cross sections makes it possible to reconstruct the following pattern. At node A, *Fig. 10*, there are twelve bundles and two large detached strands opposite the two conspicuous gaps in the eustele. Somewhat below the node there are eleven or ten strands, *Fig. 11*, due to the inclusion of the two (d) traces and the fusion of three or four pairs of (a) and (b). In some cases the (a) and (b) strands fuse at a lower level and there are fourteen bundles at this level. At a lower level the number of bundles is commonly twelve due to separation of the (d) strands into their constituent halves and the fusion of all four pairs of (a) and (b) strands, *Fig. 12*. At nodes B and C, the fusing of the bundles (ab) and (c) occurs above the nodal level. The total number of bundles at these levels was therefore eight only, *Figs. 13 & 17*.



FIGURES 10–15. Cross sections of the mature part of a shoot of *Chimonanthus praecox*, cut at the successive levels shown in FIGURE 16. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

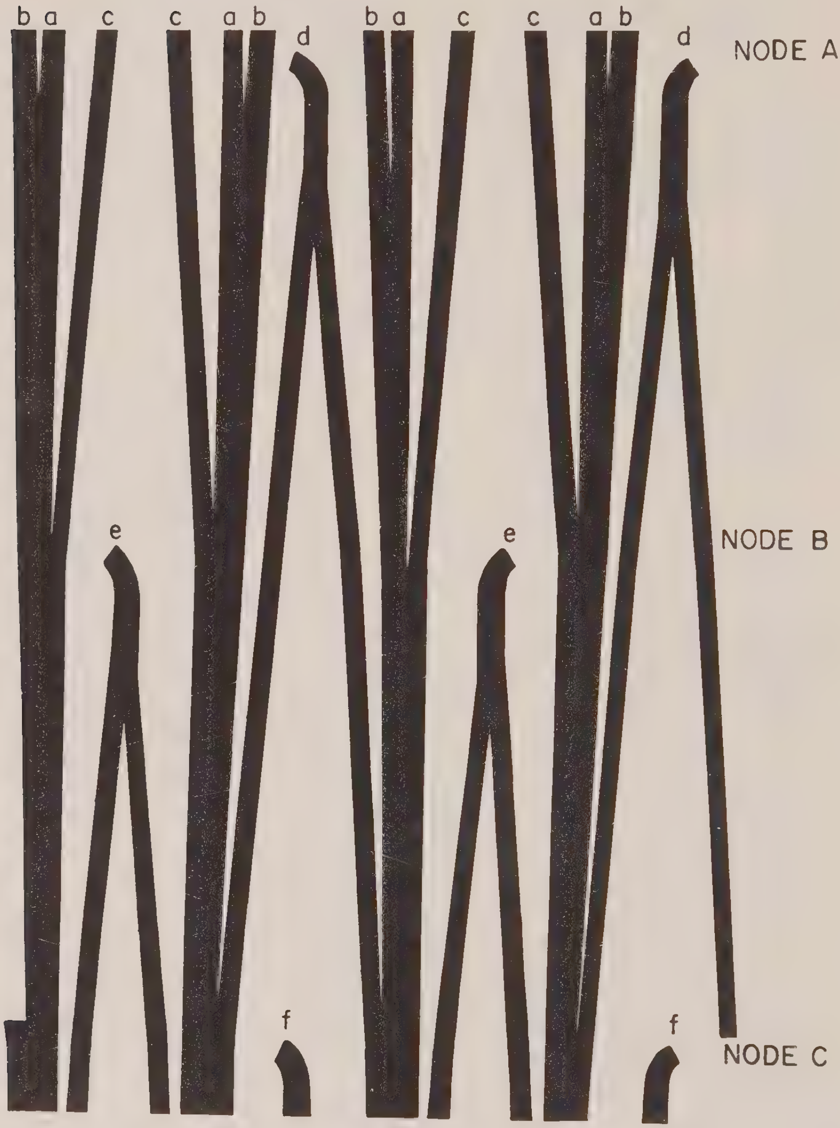


FIGURE 17. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Chimonanthus praecox*.

INDEPENDENCE OF THE CORTICAL SYSTEM OF VASCULATURE

The course and behavior of the cortical vascular strands in our material — we have not studied the floral axis as yet — is in general agreement with that reported by previous investigators. Each of the four cortical strands has three lateral branches at the nodal level, *Plate II*. One of these runs independently through the petiole and into the marginal basal part of the lamina. The other two unite with the large median strand in the base of the petiole. There are in addition two transverse connections between the cortical strands at the nodal level in stems of *Calycanthus*, *Plate II, A*. These connections occur in the two opposite sides of the stem which do not form foliar gaps at the node, *Fig. 6*. However, in our specimens of *Chimonanthus praecox* they are very tenuous in some of the immature nodes. They are absent in others and in all mature stages examined, *Plate II, B*. In some cases, there are indications that early tenuous inter-strand connections may possibly have been disrupted during subsequent lateral enlargement of the stems. There are no connections in our material of immature and mature stems between the cortical vascular strands and the central eustele, except in the epicotyl between the cotyledonary node and the first foliar node.

Seedlings grown from seed labeled *Calycanthus floridus* and *C. laevigatus* have the fundamental, double-trace, unilacunar, cotyledonary structure that occurs in so many dicotyledonous families, Bailey (1). The branches of the two discrete traces may extend independently throughout the lamina of a cotyledon or certain of their branches may approximate giving the appearance of a midvein.

DISCUSSION AND CONCLUSIONS

Our investigations of both genera of the Calycanthaceae indicate that these plants belong in the category of unilacunar dicotyledons which have been shown in recent years [4] to have leaves and cotyledons that are vascularized by ramifications of two traces that are related to independent parts of the eustele. In certain representatives of this category, e. g. *Ascarina*, *Austrobaileya*, *Trimenia*, the two traces and their branches extend at times independently throughout the stem, petiole and lamina of the leaf. In many others, approximation or apparent fusion of the two vascular strands, or of certain of their branches, occurs at various levels of the stem, petiole or lamina,

The Calycanthaceae are significant in the latter connection exhibiting various stages of approximation and fusion in mature cotyledons and during the ontogenetic development and maturation of the stem and its foliar appendages. In addition, the two genera of the family are of interest in illustrating a special trend of modification of the basic double-trace, uni-

[4] In this connection see Bailey and Swamy (2), Money, Bailey & Swamy (9), Swamy & Bailey (12), Swamy (11), Marsden & Bailey (7), Bailey (1).

lacunar form of vasculature, viz. the development of a superimposed independent system of cortical strands. In none of our material of seedlings and adult plants is there any evidence indicative of the derivation of the cortical system by modification of trilacunar or multilacunar structure.

The double-trace, unilacunar structure of the primary vascular cylinder of the Calycanthaceae, which so clearly resembles that of representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae, is suggestive of relationship between these families, but taken *by itself* is not conclusive proof of *close* affinity since the structural similarities might be due to parallel or convergent evolution or to the persistence of a primitive form of vasculature — such as occurs in *Ginkgo biloba*, Gunckel & Wetmore (5), certain species of *Ephedra*, Marsden & Steeves (8), and other gymnosperms — in dicotyledons of relatively remote relationship. It should be noted in this connection that a fundamentally similar form of vasculature occurs within the Verbenaceae, Labiatae and Solanaceae. Only when considered in connection with the *totality* of evidence from all organs and parts of the plant do vascularization patterns become reliably significant in studying problems of phylogeny and natural relationships.

As emphasized by Money, Bailey & Swamy (9), there are two distinct categories of woody ranalian families which have ethereal oil cells and monocolpate pollen or pollen which has evolved by phylogenetic modification of such grains. One of these groups of families — the Winteraceae, Degeneriaceae, Magnoliaceae (sensu stricto), Himantandraceae, Annonaceae, Eupomatiaceae, Myristicaceae — are characterized by having trilacunar or multilacunar nodes. The other category — the Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, Lactoridaceae — have double-trace unilacunar nodes or unilacunar modifications of this basic form of vasculature. Our investigations of the eustele of the Calycanthaceae when considered in the light of a summation of collateral evidence indicates that the family belongs in the second category of ranalian families and is more closely related to them than to any of the families in the first category.

ACKNOWLEDGMENTS

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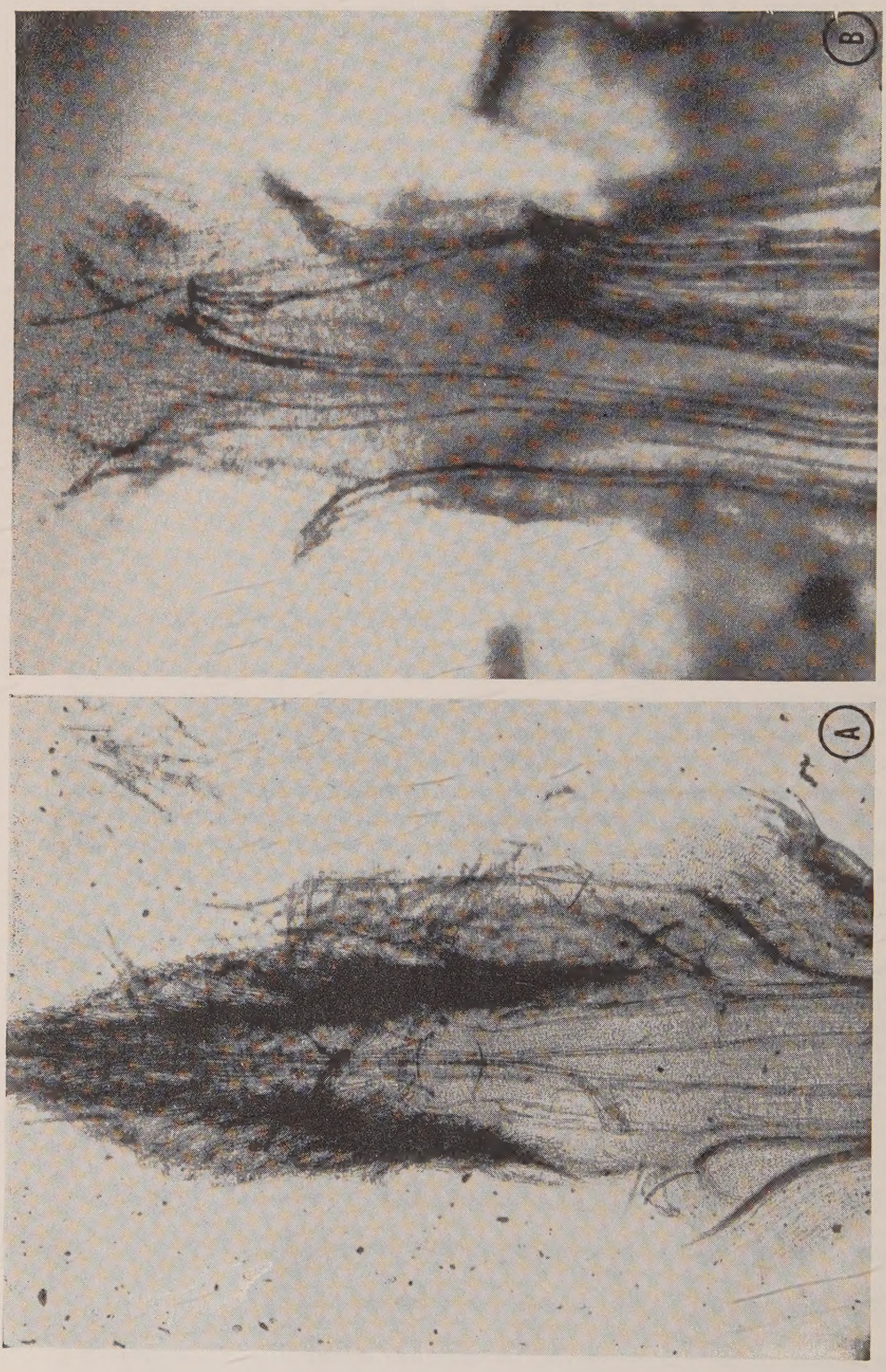
DESCRIPTIONS OF PLATES

PLATE I

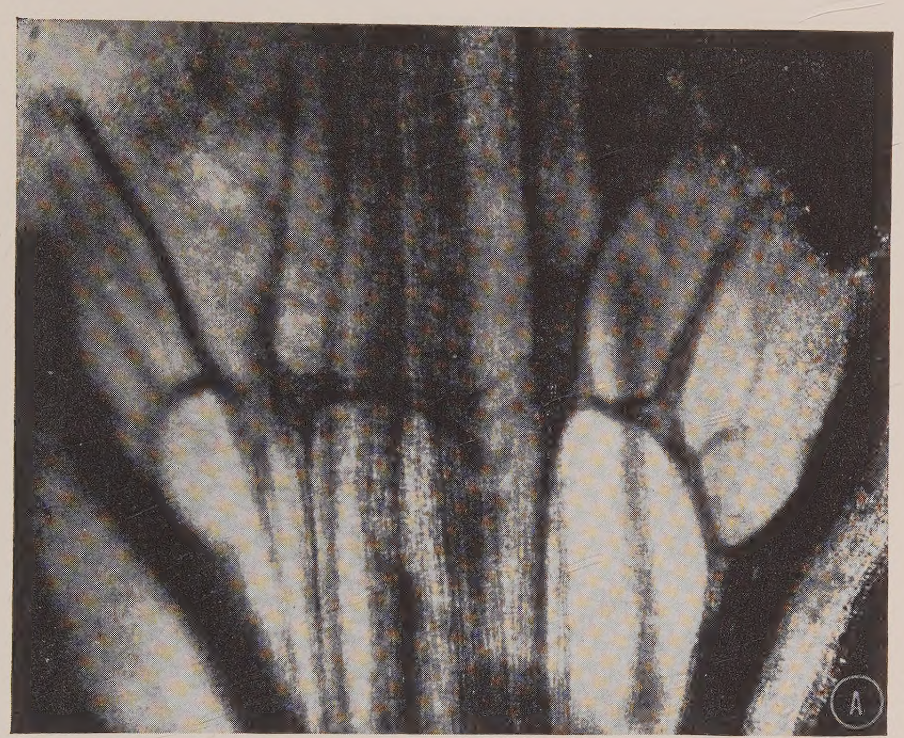
Cleared terminal parts of young shoots. The epidermis and some of the cortical tissue have been removed. A. *Calycanthus fertilis* var. *laevigatus*, showing two separate traces entering a young leaf. B. *Chimonanthus praecox*, showing the vascular strands of the eustele.

PLATE II

Mature nodes after clearing and removing the epidermis. A. *Calycanthus floridus* var. *ovatus*, showing lateral connection between two cortical strands and the branches which enter the leaves. B. *Chimonanthus praecox*, showing the absence of transverse connection between the two cortical strands.



Fahn and Bailey, Calycanthaceae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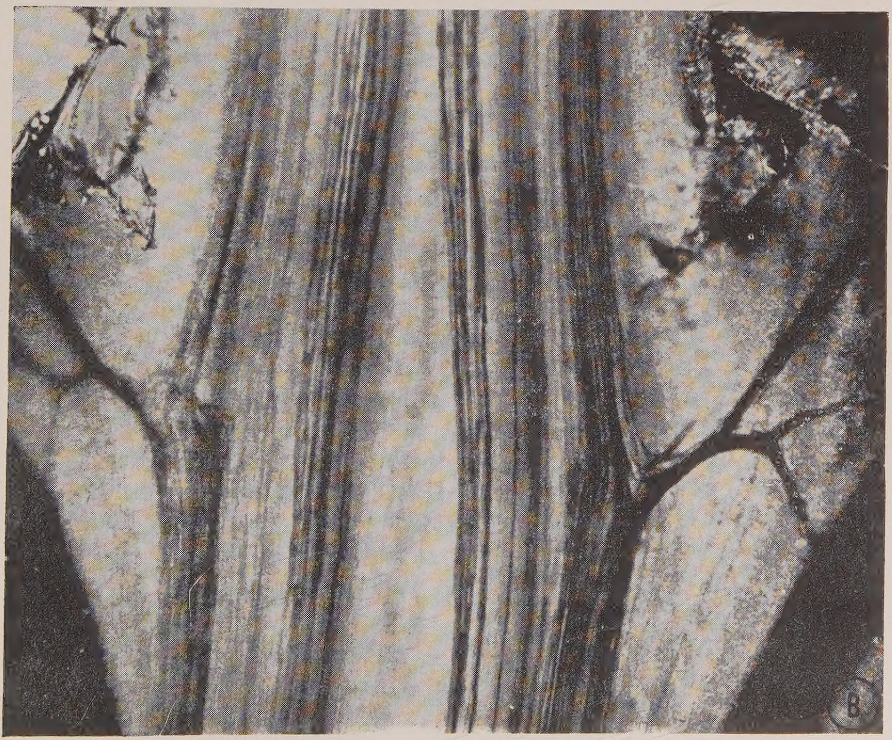
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